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A COMPARATIVE STUDY OF SPIRACULAR STRUCTURE AND MECHANISMS IN SOME HYMENOPTERA

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With 12 Plates and 4 Text-figures

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I. Introduction

Very little is known of the structure and mode of action of the spiracles in the Hymenoptera. Snodgrass (1956), Wohlgemuth (1929) and Morison (1928) have provided detailed accounts of the spiracles and spiracular musculature of *Apis mellifera* L., and Duncan (1939) gives a good description of their condition in *Vespula pennsylvanica* Saussure. Apart from these contributions and the less accurate or incomplete studies of Krancher (1881), Janet (1902) and

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Embleton (1904), information is limited to such external features as have interested taxonomists and to some indications of variations in the number of gastral spiracles in the various groups of Parasitica (*e.g.* Richards, 1956). The present paper aims at describing, in a systematic way, the structure and probable mode of action of the spiracles in representatives of all the superfamilies of Hymenoptera and at indicating some of the implications which their structure has for the classification of the order. It is to be followed later by a comparative account of the tracheal system of the Hymenoptera.

I am greatly indebted to Professor O. W. Richards for suggesting the subject of this investigation, for his interest in its progress and for providing some of the specimens studied. I also wish to thank Mr. R. B. Benson of the British Museum (Natural History) for providing specimens of some of the Symphyta dealt with, and Mr. R. G. Davies for his assistance and advice.

II. Material and Technique

Most of the material was freshly collected, but a few species were studied only from dried specimens. In all, species of 64 genera, representing 25 families in the classification of Imms (1957), were studied.

Examination of live or freshly killed insects with freely exposed spiracles revealed the existence of external movable parts when present. For anatomical studies involving musculature, the sclerites and other structures surrounding the spiracular area were cut out and fixed in Bouin's fluid. Purely cuticular structures were studied after maceration in warm potassium hydroxide solution. Heavily pigmented preparations were decolorised with Diaphanol, chlorine or hydrogen peroxide and, when necessary, afterwards stained with acid fuchsin. Dissections of fixed or macerated material were made after dehydrating and clearing in clove oil so as to leave the relevant spiracular structure and its musculature intact. It was found possible by pressing and pulling at various parts to appreciate something of their relative flexibility, and this helped to suggest the mechanisms of spiracular movement. Pulling delicately at the muscles and their associated apodemes also helped to determine their role in spiracular movements.

III. Terminology and Definitions

In order to describe concisely the spiracles of the Hymenoptera it has been found necessary to develop some new terms or to use older ones in a more precise sense. The following alphabetically arranged list defines some of the structures encountered, but it should be made clear that not all these are present in a given spiracle.

(1) *Circumperitremal area* (Pl. XII, fig. 78, *Cp*).—An area of sclerotised cuticle forming that part of the *collar* which lies between the *peritreme* and the *rim*. When bowl-shaped, *i.e.* externally concave, it is also referred to as the *spiracular depression*. It is sometimes a little convex externally (e.g. *Anthophora*) and it may not surround the peritreme completely (e.g. *Stelis*, fig. 81).

(2) *Collar* (Pl. XII, fig. 78).—A complex sclerite which normally surrounds the *peritreme*. When complete it comprises three parts : (*a*) the *circumperitremal area*, which is bounded peripherally by (*b*) the externally visible *rim* and by (*c*) the corresponding internal *flange*.

(3) *Flange* (Pl. XII, fig. 78, *F*).—The internally inflected periphery of the circumperitremal area. It is strongly sclerotised, rigid, and serves as a site for the origin of the occlusor muscles.

(4) *Peritreme* (Pl. XII, fig. 78, *P*).—The sclerotic ring immediately surrounding the spiracular aperture. It may be produced into the following structures: (*a*) the *operculum*, a flap-like, approximately circular plate which is more or less movable and is able to close the spiracular opening (Pl. 11, fig. 71, *OP*); (*b*) a pair of *lids*, which project external to the peritreme and can be moved to close the spiracular opening; (*c*) one or two *membranous flaps* which lie internal to the peritreme and may be apposed to each other by the occlusor muscle, so closing the spiracle; they are usually, but not always, present in the second thoracic spiracle; (*d*) one or two immovable, externally convex *lips*, which are perhaps homologous with the lids but are functionally different.

(5) *Posterior pronotal apodeme* (Pl. IV, fig. 24).—A rigid sclerotised apodeme arising from the posterior edge of the pronotum ventral to the spiracle. It forms a site for the attachment of the occlusor muscle in many Hymenoptera.

(6) *Posterior pronotal inflection* (Pl. V, figs. 30, 31).—A flexible apodeme, found only in the Evanioidea, which arises from the posterior edge of the pronotum dorsal to the spiracle. An occlusor muscle arises from it.

(7) *Pronotal occlusor sclerite* (Pl. IV, fig. 29, *PS*).—A large sculptured sclerite which is flexibly articulated internally to the pronotum.

(8) *Rim of the collar* (Pl. XII, fig. 78, *Ri*).—The externally raised peripheral margin of the circumperitremal area; completely or partially sclerotised. It occurs only in the second thoracic spiracle and then not always.

(9) *Vestibule* (Pl. XII, fig. 79, *V*).—Found in the first thoracic spiracle of some Apoidea and Evanioidea. It is a cavity external to the peritreme (as opposed to the *atrium*, which is internal to the peritreme) and is formed by the close apposition of the inner face of the pronotal lobe to the mesepisternum.

IV. Systematic Survey

A. Symphyta

There are two thoracic and eight abdominal spiracles in all the species studied.

Xyeloidea

(1) *Xyelidae*

Xyela julii (Brébisson)

First thoracic spiracle (Pl. I, fig. 1).—This spiracle lies in the membrane between the pronotum and the mesepisternum and has a lightly sclerotised peritreme, the anterior part of which is covered with spiny projections. Arising from the peritreme are two membranous outgrowths, the spiracular lids (*Ld*). Ventral to the two lids is inserted an acicular occlusor muscle arising from a sclerotised ridge. Its contraction brings the two lids near to each other. The elasticity of the parts allows the opening to be re-established.

Second thoracic spiracle (Pl. I, fig. 2).—This lies in the membrane close to the notch formed by the posterior edge of the mesepimeron and resembles the anterior thoracic spiracle in structure and function, except that the muscle is fan-shaped and takes its origin from a sclerotised ridge ventral to the spiracle.

Abdominal spiracles (Pl. I, figs. 3, 4).—These are situated on the sides of the terga of the first eight segments. The first pair is slightly different in shape, being more circular with larger levers; the remaining ones are uniform in structure and mechanism.

Each has a strongly sclerotised peritreme which leads to a shallow atrium from which arise two short blunt levers. The tracheal opening is guarded by the closing valve between the levers. A parallel-sided occlusor muscle is attached between the two levers and its contraction brings the closing valve forwards to close the spiracular opening. The dilator muscle, running from the ventral lever to a posterior notch on the appropriate tergite, acts antagonistically.

Siricoidea

(2) *Siricidae*

Sirex juvencus (L.)

First thoracic spiracle (Pl. I, figs. 5, 6).—This is situated posterior to the pronotal lobe, which does not conceal it, and lies below the episternal parapterum. The spiracle has two tracheal openings; the ventral one is larger and oval, the dorsal one circular and smaller. Each opening is surrounded by a slightly sclerotised peritreme and has two lids lying anterodorsal and posteroventral respectively; both are membranous in texture and arise directly from the peritreme. An acicular occlusor muscle arises from an apodeme of the mesepisternum and inserts on the ventral margin of the lids by one or two elastic tendons. The contraction of the muscle would result in both sets of lids (which are apparently continuous) being brought together so as to close the spiracular openings.

Second thoracic spiracle (Pl. I, figs. 7, 8).—This is situated posterior to the mesepimeron and has the usual single opening, inclined to the axis of the body. The spiracular area is demarcated from the surrounding membrane by a sclerotised plate with a thick sclerotic rim. Externally there is a relatively immovable posterior lid arising from the well marked peritreme. Closing is brought about by the movable internal lid, the movement of which is controlled by a fan-shaped occlusor muscle, which when it contracts raises the lid to close the spiracle. Opening occurs owing to the elasticity of the spiracular parts.

Abdominal spiracles (Pl. I, fig. 9).—These are situated on the sides of the first eight tergites. Each has an irregularly oval peritreme leading into a shallow atrium which is produced into two short levers between which is a closing valve. The cylindrical occlusor muscle is inserted between the two levers. The contraction of the muscle pushes the closing valve backwards to close the tracheal opening. The spiracle is opened by the contraction of the parallel-sided dilator muscle and simultaneous relaxation of the occlusor muscle.

(3) *Xiphydriidae*

Xiphydria camelus (L.)

First thoracic spiracle.—This lies in membrane behind the pronotum and is similar in structure and mechanism to the corresponding spiracle in *Sirex*.

Second thoracic spiracle.—These are similar to the corresponding spiracles in *Sirex* except that the anterodorsal lid is small and immovable whereas the posteroventral one is large and alone movable.

Abdominal spiracles.—These are large and lie on the sides of the tergites. Each is an irregularly oval aperture leading into an indistinct atrium. The latter is produced into a single ventral lever and has, to its dorsal side, a rigid sclerotic process, the manubrium. Between the two lies a cylindrical occlusor muscle. The parallel-sided dilator muscle runs from the lever to a posterior notch on the tergum. Contraction of the occlusor muscle closes the tracheal opening by pushing the closing valve forwards, while its relaxation with contraction of the dilator muscle opens the tracheal opening.

Cephoidea

(4) *Cephidae*

(a) *Cephus cultratus* Eversmann ; (b) *Cephus pygmaeus* (L.)

The position, structure and mechanism being similar in both species, they are dealt with together.

First thoracic spiracle (Pl. II, figs. 10, 11).—As in *Sirex* and *Xiphydria*, there are two distinct tracheal openings on each side in the intersegmental membrane between the pronotum and mesepimeron. Each pair of openings is covered by three plates, the spiracular lids. These are probably homologous with the lids since (1) the second thoracic spiracle has the usual two lids with similar sculpturing, (2) sculpturing on the spiracular lids is not uncommon in Hymenoptera, and (3) the insertion of the muscle indicates that the dorsal and ventral lids form the movable part of the spiracle. The contraction of the acicular occlusor muscle brings the two movable lids near to each other to close the spiracle. There is no dilator muscle.

Second thoracic spiracle (Pl. II, fig. 12).—Each is a simple circular aperture lying in membrane just behind the mesepimeron. The spiracular opening is surrounded by a slightly sclerotised peritreme, from which arise two lids. Both are heavily sculptured and fused together at the anterodorsal part of the spiracle. A fan-shaped occlusor muscle attached to this region brings the two lids near each other to close the spiracle. Opening occurs through relaxation of the parts.

Abdominal spiracles (Pl. II, fig. 13).—Each is a large oval opening on the sides of the first eight tergites. The discrete peritreme has short hairs on the anterior side and leads into a shallow atrium from which two large levers arise. A parallel-sided occlusor muscle runs between them and a similarly shaped dilator runs from the ventral lever to the posterior notch on the tergum. Contraction of the former muscle constricts the tracheal opening, the latter acting as an antagonist to it.

Tenthredinoidea

(5) *Diprionidae*

(a) *Diprion pini* (L.)

First thoracic spiracle (Pl. II, fig. 14).—This is situated in the inflected part of the posterior lobe of the pronotum which forms an arch completely enclosing

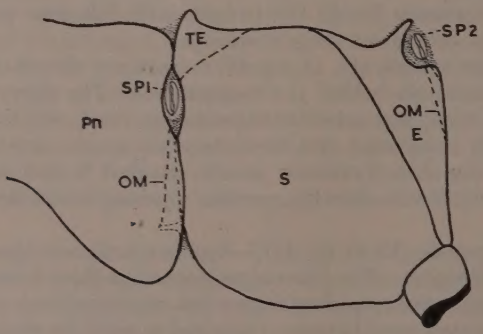
the spiracle. The opening is oval in outline and its outer edge forms a distinct lid on which a slender acicular occlusor muscle is inserted. This muscle takes its origin on a posterior pronotal apodeme a short distance below the spiracle. Contraction of the muscle brings the lid close to the opening. The elasticity of the parts allows the opening to be re-established.

Second thoracic spiracle.—This is nearly as large as the first and lies in the membrane just behind the notch formed by the posterior edge of the mesepimeron. It resembles the corresponding spiracle in *Xyela* except that the anterior lid is narrow and more rigid than the posterodorsal one.

Abdominal spiracles (Pl. II, figs. 15, 16).—These lie on the sides of the first eight terga. The first pair is the largest and they become progressively smaller in the posterior segments, the smallest being two-thirds the diameter of the largest. Each is surrounded by a strongly sclerotised peritreme, the posterior wall of which projects forwards and is tucked under the anterior one. The flap thus forms a closing valve which is membranous centrally, while its edge is thickened to form a sclerotised rim. A large strong lever is present which moves this valve; it arises from the internal side of the anterior lip and the internal side of the valve itself. Arising from the apex of the lever and running to a small tergal ridge, is a short muscle which, by its contraction, opens the spiracle. There is no occlusor muscle, closing apparently being due to the elasticity of the various structures.

(b) *Neodiprion sertifer* (Geoffroy)

Apart from minor differences, all the spiracles resemble the corresponding ones in *Xyela*. Text-figure 1 shows the lateral view of thoracic sclerites in relation to the spiracles.



TEXT-FIG. 1.—*Neodiprion sertifer* (Geoffroy). Lateral view of thoracic sclerites in relation to the spiracles.
(For explanation of lettering see page 520).

(6) *Tenthredinidae*

(a) *Tenthredo arcuata* Forster

First thoracic spiracle (Pl. III, fig. 17).—Each is situated between the pronotum and the mesepisternum. Arising from the sclerotised peritreme are two movable lids, of which the anterior one is more strongly sclerotised. An acicular occlusor muscle runs from the base of the two lids to the anterior ridge of the

mesepisternum. The mechanism is similar to the corresponding spiracle in *Xyela*.

Second thoracic spiracle.—The regulatory apparatus resembles that of the anterior thoracic spiracle except that the occlusor muscle is fan-shaped.

Abdominal spiracles (Pl. III, fig. 18).—Each has a distinct sclerotised peritreme. The anterior lip of the spiracle is raised and slants towards the opening, which forms a narrow crescentic slit on the posterior side. The opening leads to a shallow atrium, the ventral side of which is produced into a curved lever. Between the lever and the atrium is a short parallel-sided occlusor muscle, contraction of which causes the closing valve to move and so close the tracheal orifice. Arising from the apex of the lever and running to a small tergal ridge is a short dilator muscle which opens the valve.

(b) *Dolerus gonager* (Fabricius); (c) *D. niger* (L.); (d) *D. aeneus* Hertig

These are treated together as no important differences were found in their spiracular structure and mechanism.

First thoracic spiracle (Pl. III, fig. 19).—These are large openings lying between the pronotum and the mesepisternum. Each has a sclerotised peritreme which gives rise to peculiar raised lids. The anterior one is broad dorsally and narrow ventrally, a condition exactly opposite to the posterior lid. The two lids are fused ventrally and from this point an acicular occlusor muscle runs to the posterior wall of the pronotum. Contraction of the muscle moves the lids so as to overlap each other; relaxation results in their moving apart so as to open the spiracle.

Second thoracic spiracle.—The structure and mechanism is as described above for the first thoracic spiracle.

Abdominal spiracles (Pl. III, figs. 20, 21).—These vary slightly in shape, there being two main types. Each has a distinct sclerotised peritreme leading to a shallow atrium, the ventral wall of which is produced into a lever with a closing valve. The lever is either long or short and curved. Between it and the dorsal rim of the spiracle (atrium) runs a parallel-sided occlusor muscle the contraction of which presses the closing valve against the opposite side of the tracheal opening. The opening of the spiracle is brought about by the contraction of the dilator muscle.

(c) *Taxonus agrorum* (Fallén)

First thoracic spiracle.—This resembles the corresponding spiracle in *Dolerus* except that the occlusor muscle arises on an apodeme of the posterior wall of the pronotum.

Second thoracic spiracle.—This resembles the first in structure and mechanism. The fan-shaped occlusor takes its origin from an internal ridge on the mesepimeron.

Abdominal spiracles (Pl. III, figs. 22, 23).—Each has an oval sclerotised peritreme. The anterior wall projects backwards and is tucked under the posterior one, leaving a small spiracular opening dorsally. This external opening leads to a shallow atrium, the dorsal side of which is produced ventralwards into a lever. Arising from the apex of the lever, and running to a small tergal ridge, is a short parallel-sided muscle which by its contraction opens the spiracle. Relaxation of the muscle closes the tracheal opening.

B. APOCRITA

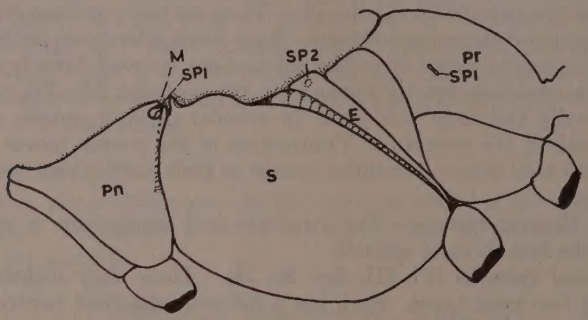
Ichneumonoidea

There are two thoracic, one propodeal and seven gastral pairs of spiracles, of which the first thoracic spiracle is freely exposed, the second concealed by the mesepimeron and the remainder, except the last one, freely exposed.

(7) *Ichneumonidae*

(a) *Amblyteles* sp.

First thoracic spiracle (Pl. IV, fig. 24).—This lies at the posterodorsal corner of the pronotum which is here provided with a small notch and inflected to form a pocket-like cavity. Towards the base of the cavity lies the circular spiracular aperture, surrounded on its outer side by the main sclerotisation of the pronotum and on the inner by the pronotal occlusor sclerite. The latter is



TEXT-FIG. 2.—*Amblyteles* sp. Side view of thorax showing the position of the spiracles.

flexibly articulated with the dorsal and posterior wall of the pronotum. To the former is attached an acicular occlusor muscle which takes its origin from an apodeme of the posterior pronotal wall. The contraction of the muscle pulls the flexibly articulated sclerite down to close the spiracle and its relaxation opens it owing to the elasticity of the various parts. Text-figure 2 shows the side view of the thorax with the position of the spiracles.

Second thoracic spiracle (Pl. IV, fig. 25).—Each lies concealed beneath the mesepimeron, the inner surface of which holds the inconspicuous peritreme. The remaining sides are surrounded by pleural membrane. A flat lid-like operculum is attached ventrally to the ridge of the mesepimeron and a fan-shaped occlusor muscle arises on its posterior ridge. The muscle is connected to the spiracular operculum by an elastic apodeme. Contraction of the muscle pulls the lid to close the spiracle and, as the parts are sufficiently elastic, opening occurs when the muscle relaxes.

Propodeal spiracle (Pl. IV, fig. 26).—Each lies freely exposed on the propodeum and is broadly oval with a well defined peritreme leading into a shallow atrium, which in turn opens into the spiracular trachea. The atrial wall gives

rise to a single ventral lever and a small dorsal manubrium. A cylindrical closing muscle runs between the apex of the lever and the manubrium and a similar dilator from the lever to the sternum. Contraction of the closing muscle occludes the tracheal opening and the dilator acts as an antagonist to it.

Gastral spiracles (Pl. IV, fig. 27).—These are situated on the terga of the first seven segments. Each has a circular opening surrounded by the peritreme leading into an almost spherical atrium. The atrial walls are produced into two elongate levers between the apices of which is a cylindrical occlusor muscle. The similarly shaped dilator muscle runs from the ventral lever to an apodeme on the sternum. Contraction of the muscle closes the tracheal opening which is opened by the antagonistic action of the dilator.

(b) *Pimpla instigator* (Fabricius)

First thoracic spiracle (Pl. IV, fig. 28).—This is similar to the corresponding spiracle in *Amblyteles* except that the occlusor muscle is connected by elastic apodemes to the two sides of the pronotal occlusor sclerite.

The remaining spiracles are similar to the corresponding spiracles in *Amblyteles* except for minor details.

(c) *Lissonota* sp.; (d) *Ophion* sp.; (e) *Nemeritis canescens* (Gravenhorst)

The spiracles of these species are similar in structure and mechanism to the corresponding spiracles of *Pimpla instigator*.

(8) *Braconidae*

The thoracic spiracles differ from those of the Ichneumonidae in three points:

(i) An atrium of extremely variable shape is present in the first thoracic spiracle of all three species studied.

(ii) The spiracles are concealed in *Alysia* by the extension of the dorsoposterior corner of the pronotum; in the remaining species they are freely exposed.

(iii) The second thoracic spiracle differs from the corresponding spiracles in Ichneumonidae

(a) *Brachistes* sp.

First thoracic spiracle (Pl. IV, fig. 29).—Each is freely exposed with an opening surrounded externally by the pronotal sclerotisation and internally by a flexibly articulated pronotal occlusor sclerite, the peritreme being obviously fused with these parts. The opening leads into a broad and well developed atrium with thin membranous walls. The base of the atrium opens into the spiracular trachea. An acicular occlusor muscle is attached to the two ends of the occlusor sclerite by means of elastic apodemes; its contraction closes the opening. Opening of the spiracle occurs through the elasticity of the parts when the occlusor muscle relaxes.

Second thoracic spiracle.—This is concealed beneath the mesepimeron and has a well developed peritreme which gives rise to two membranous flaps, to the dorsal side of which lies a small elastic plate to which a fan-shaped occlusor muscle is attached. The muscle arises on a ridge at the posterior side of the

spiracle. Contraction of the muscle pulls the membranous flaps closely together to close the spiracle.

Propodeal spiracle.—In all important respects these resemble the corresponding spiracle in *Amblyteles.*

Gastral spiracles.—Each is similar to the propodeal spiracle except that the atrium is deeper.

(b) *Blacus* sp.

All spiracles resemble the corresponding ones in *Brachistes* except for some variation in the structure of the atrium.

Evanioidea

There are two thoracic, one propodeal and one gastral pair of spiracles.

(9) *Gasteruptiidae*

(a) *Gasteruption jaculator* (L.); (b) *G. assectator* (L.)

These are dealt with together as they do not show any important differences.

First thoracic spiracle (Pl. V, figs. 30, 31).—This lies concealed beneath the posterior lobe of the pronotum, its opening being in the membrane between pronotum and mesepisternum. It has a well developed sclerotised peritreme, near the dorsal side of which arises a hook-like process, which it is perhaps best to regard as a pronotal inflection since it arises from the posterior wall of the pronotum just above the peritreme. The latter leads into an atrium, the dorsal and posterior walls of which are membranous and flexible. The tracheal opening is situated at the base of the atrium. An acicular occlusor muscle is inserted between the tip of the posterior pronotal inflection and a ventral apodeme of the pronotum. Contraction of the muscle pulls the flexible dorsal and posterior walls of the atrium to cover the tracheal opening; the elasticity of the parts allows the opening to be re-established.

Second thoracic spiracle (Pl. V, fig. 32).—Each is a small slit-like opening just above the infolded membrane between the mesepimeron and the metapleuron. The external opening has a thick peritreme surrounded by a collar and leads into a shallow atrium, the walls of which are thin and membranous and form the closing membranous flaps. Ventrally to the flaps is an elastic plate the walls of which form a ring around the tracheal mouth. The fan-shaped occlusor muscle takes its origin on the ventral edge of the collar and its contraction brings the flaps together to close the spiracular opening. As the parts are elastic relaxation of the muscle opens the spiracle.

Propodeal spiracle (Pl. V, fig. 33).—These are situated on the dorsolateral side of the propodeum. Each has a thick peritreme the outer rear lip of which projects anteriorly, making the spiracular opening slit-like. The ventral surface of the shallow atrium is produced into a long lever and the dorsal side into a short manubrium. Between the two lies a closing valve, and a parallel-sided occlusor muscle runs from the tip of the manubrium to the lever. The dilator runs ventrally and caudally from the apex of the lever to the sternum. Contraction of the occlusor pushes the closing valve forwards to close the spiracle,

while contraction of the dilator and antagonistic relaxation of the occlusor opens the spiracle.

Gastral spiracles.—These are closely similar in structure and mechanism to the propodeal spiracle.

(10) *Evaniidae*

Zeuxevania splendidula (Costa)

First thoracic spiracle (Pl. V, fig. 34).—This lies beneath the posterodorsal corner of the pronotum, partially concealed by the latter. It is a circular opening at the base of a pocket-like vestibule which communicates with the exterior by a small aperture formed from a groove in the pronotum. The true spiracular opening leads into an atrium with extremely delicate and membranous walls, and bearing, dorsally and ventrally, sclerotised callipers between which is a membranous flap acting as a closing valve. To the ventral calliper is attached an acicular occlusor muscle. The two callipers are joined by an elastic apodeme-like structure. Contraction of the occlusor muscle pulls the two callipers, so causing the membranous flap to close the tracheal opening; relaxation of the muscle opens the spiracle.

Second thoracic and propodeal spiracles are broadly similar to the corresponding spiracles in *Gasteruption*.

Gastral spiracles (Pl. V, fig. 35).—A single pair is situated on the eighth tergite. Each has an oval opening leading into a large atrium which is produced into two knob-like levers. At the base of the atrium is the tracheal opening. A cylindrical occlusor muscle is inserted between the two levers. The dilator of the same shape runs from the ventral lever to the lateral edge of the tergite. Contraction of the occlusor pinches the tracheal opening, while the contraction of the dilator reopens it.

Cynipoidea

In the species studied there are only three pairs of spiracles, one prothoracic, one propodeal and one gastral (on the eighth tergum).

(11) *Cynipidae*

(a) *Neuroterus kollari* (Hartig)

First thoracic spiracle (Pl. VI, figs. 36, 37).—This lies slightly below the posterodorsal corner of the pronotum. The spiracular opening is in a deep groove formed by the external and the inflected internal wall of the pronotum, and hence concealed by the former. It has a thick peritreme leading into a highly sclerotised and sculptured atrium with thick bristle-bearing walls. This leads into another large cavity, the so-called secondary atrium, with smooth, thin walls. At its base are situated membranous callipers, to the internal arm of which is attached a long tendon with an occlusor muscle of an acicular shape. When this muscle contracts the membranous calliper turns from its normal position, closing the passage between the atrium and trachea.

Propodeal spiracle (Pl. VI, fig. 38).—This is bean-shaped in outline with a raised rear lip which reduces the external opening to a lateral elongate slit. The opening leads into a shallow thick-walled atrium, the internal posterior wall being covered with thick spiny bristles. There are two large levers arising

from the anterior and posterior walls and between the two levers lies a closing valve. The parallel-sided occlusor muscle is inserted between the apices of the two levers. The dilator muscle is short and runs from the ventral lever to the internal ridge of the propodeum. The contraction of the occlusor closes the tracheal opening and antagonistic contraction of the dilator opens it.

Gastral spiracles.—These are a single pair on the eighth tergite and are normally concealed owing to the telescoping of the segments. Each is a circular opening surrounded by a thick peritreme leading into a shallow atrium, the walls of which have short hairs, and which is produced into two long levers. An occlusor muscle is inserted between the apices of the two levers and the dilator runs from the ventral lever to the posterior tergal edge. Contraction of the occlusor pushes the closing valve forwards to pinch the tracheal orifice and antagonistic contraction of the dilator pulls the closing valve to open the orifice.

(b) *Andricus gemmatus* Adler ; (c) *A. testacipes* Hartig

The position, structure and mechanism are similar in these species to the corresponding spiracles in *Neuroterus*.

(d) *Rhodites rosae* (L.)

First thoracic spiracle (Pl. VI, fig. 39).—This resembles the corresponding spiracle in *Neuroterus* except that the atrium is much more distinctly divided. The secondary part is membranous and short and has at its base a membranous calliper which is produced into an elastic apodeme to which is attached an acicular occlusor muscle.

Propodeal and gastral spiracles do not show any important differences from the corresponding spiracles in *Neuroterus*.

(e) *Biorrhiza pallida* (Olivier)

First thoracic spiracle.—Each is similar to the corresponding spiracle in *Neuroterus* except that the calliper is curved and sclerotised.

Propodeal spiracle.—Each is essentially similar in structure and mechanism to the corresponding spiracle in *Neuroterus* except that the rear lip is absent and the levers are unequal.

Gastral spiracle.—The structure and mechanism is as described above for the corresponding spiracle in *Neuroterus*.

Chalcidoidea

There are one thoracic, one propodeal and one gastral pair of spiracles.

(12) *Pteromalidae*

(a) *Mormoniella vitripennis* (Walker) ; (b) *Anisopteromalus calandrae* (Hau.)

These are treated together as they do not show any important differences.

First thoracic spiracle (Pl. VII, fig. 40).—Bucker (1948) notes only the position of these spiracles in the intersegmental membrane just below the flanges formed by the inflected cuticle for the articulation with the mesonotum. However, it may be added that they lie partly concealed beneath the pronotum.

Each has a clearly sclerotised ring-like peritreme. There is no atrium, the peritreme being followed immediately by the trachea. The peritreme is capable of being covered by a thin, weakly sclerotised operculum. An acicular muscle, arising on an apodeme from the operculum near its point of attachment, runs to a pronotal ridge ventral to the spiracle. Contraction of the muscle presumably lowers the operculum to close the spiracle which opens when the occlusor relaxes because of the elasticity of the parts.

Propodeal spiracle.—Each is similar in structure and mechanism to the corresponding spiracles in *Neuroterus* except that the raised rear lip is absent and curved levers give a horseshoe appearance.

Abdominal spiracle (Pl. VII, fig. 41).—Each is concealed on the side of the eighth tergite and resembles the propodeal spiracle except that it is smaller in size with a perfectly circular peritreme and a shallow atrium. The tracheal opening is pinched owing to the contraction of the occlusor muscle.

(13) *Torymidae*

(a) *Torymus cingulatus* Nees ; (b) *T. auratus* (Geoff.)

No differences in spiracular structure were found between these two species.

First thoracic and propodeal spiracles.—These are as described above for the corresponding spiracles of *Mormoniella.*

Gastral spiracle (Pl. VII, fig. 41*b*).—Each is an oval opening on the eighth tergite leading into a deep and spacious atrium which is produced into a single large lever. The occlusor muscle lies between the apex of the lever and the wall of the atrium, whereas the dilator muscle runs ventrally away from the lever. Both are cylindrical in shape. The contraction of the former closes the tracheal opening ; the latter acts as its antagonist.

Proctotrupoidea

There are two thoracic, one propodeal and no gastral spiracles in the three species studied.

(14) *Proctotrupidae*

(a) *Exallonyx* sp.; (b) *Phaenoserphus* sp.

(15) *Ceraphrontidae*

Lygocerus sp.

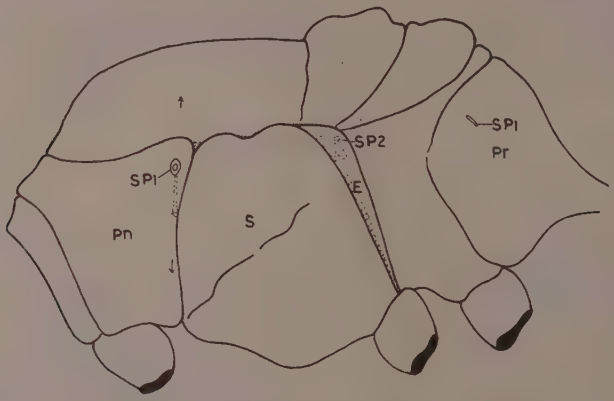
These are treated together as no important differences were found.

Prothoracic spiracle (Pl. VII, fig. 42).—Each is a roughly circular opening on the pronotum, slightly below the posterodorsal corner and before the posterior margin. Text-figure 3 shows the arrangement of sclerites in relation to the spiracles.

Each opening leads into a small atrium with thick walls and this leads to another tubular chamber or secondary atrium, the base of which opens into the spiracular trachea, and between the two is the membranous calliper. To the ventral side of the calliper is an acicular occlusor muscle attached by a short elastic apodeme. The muscle runs to the ventral apodeme of the inflected wall

of the pronotum and its contraction pulls the elastic ring so as to close the tracheal opening. Relaxation of the muscle results in the opening of the spiracle.

Second thoracic spiracle (Pl. VII, fig. 43).—Unlike the first pair these are concealed behind the mesepimeron. Each is roughly an oval opening leading into a shallow atrium, the base of which opens into the spiracular trachea. Between the two is a dorsally situated closing valve in the form of a membranous flap. A fan-shaped closing muscle is attached to it, taking its origin from a hook-like sclerotised apodeme from the ventral side of the mesepimeron. Contraction of the closing muscle pulls the dorsal wall ventrally to close the tracheal opening.



TEXT-FIG. 3.—*Exallonyx* sp. Lateral view of thorax, showing the position of the spiracles.

Propodeal spiracle (Pl. VII, fig. 44).—Each has a thick peritreme leading into a spacious and irregularly shaped atrium which is produced into a single large lever. Between the lever and a dorsal notch on the atrium is a cylindrical occlusor muscle. The cylindrical dilator muscle runs from the tip of the lever ventrally to the sternum. Contraction of the occlusor pulls the closing valve between the atrium and trachea to close the tracheal opening; contraction of the dilator and relaxation of the occlusor cause the tracheal entrance to open.

Bethyloidea

(16) *Chrysididae*

Chrysis ignita (L.)

There are two thoracic, one propodeal and four gastral pairs of spiracles.

First thoracic spiracle (Pl. VIII, fig. 45).—This lies concealed under the pubescent lobe of the pronotum. The spiracular opening is in the membrane between the pronotum and mesepisternum and is surrounded by a slightly sclerotised peritreme which gives rise to two membranous internal lids which are united ventrally. An acicular occlusor muscle runs from the ventral side to an anterior ridge on the mesepisternum. Contraction of the muscle brings the

two lids together to close the spiracular opening; elastic relaxation of the structures opens the spiracle.

Second thoracic spiracle (Pl. VIII, fig. 46).—This lies just beneath the sclerotised projection from the posterodorsal corner of the mesepimeron and is thus partially concealed. It has a thick peritreme leading into shallow atrium bounded by an anterior rigid wall and a posterior movable membranous flap, from which arises an elastic plate. A fan-shaped occlusor muscle runs from the apex of the plate to a sclerotised curved inflection of the mesepimeron. Contraction of the muscle pulls the membranous wall anteriorly to close the spiracle.

Propodeal spiracle.—This lies on the dorsolateral side of the propodeum and is similar in structure and mechanism to the corresponding spiracle of *Neuroterus* except that the ventral lever is larger than the dorsal and the dilator muscle runs from the former to a coxal apodeme.

Gastral spiracles (Pl. VIII, fig. 47).—The position of these calls for special mention. The first and last pair are situated on the sides of the second and fifth abdominal tergites, while the second and third spiracles lie on the laterotergites. Only four pairs were noted. Each has a slightly thickened peritreme leading into an ill-developed asymmetrical atrium, the ventral part of which is produced into a large lever from the apex of which the occlusor muscle runs to the notch on the atrium, while the dilator muscle runs to a ridge on the sternite. Both muscles are parallel-sided. Contraction of the occlusor pulls the lever and the closing valve occludes the tracheal orifice; antagonistic contraction of the dilator opens the spiracular valve.

Formicoidea

(17) *Formicidae*

In *Myrmica sabuleti* the second thoracic spiracle is absent, but in the remaining species there are two thoracic, one propodeal (epinotal) and seven gastral pairs.

(a) *Myrmica sabuleti* Meinert

First thoracic spiracle (Pl. VIII, fig. 48).—This lies on the posterior margin of the pronotum, the internal arch of which encloses the spiracle. It has a raised external rigid lip to the distinct peritreme, the spiracular opening being roughly oval. The external opening leads into a shallow atrium which is produced into a membranous internal closing valve. Opposite this is a small immovable fold of the atrial wall. An acicular occlusor muscle is inserted on the closing valve. The muscle takes its origin on the sclerotised peg or apodeme of the pronotum and its contraction brings down the closing valve so as to close the tracheal opening. Owing to the elasticity of the structure, relaxation of the muscle allows the spiracle to open.

Second thoracic spiracle.—This is apparently absent.

Propodeal spiracles.—These are large and oval with a thick peritreme and a well developed atrium which is produced into a large lever to the ventral side and a small manubrium dorsally. Between the two lies a cylindrical occlusor muscle. The dilator runs from the tip of the lever ventrally and caudally. Contraction of the occlusor presses the closing valve against the

opposing rigid rim of the atrium to close the tracheal opening. The dilator acts as an antagonist to it.

Gastral spiracles (Pl. VIII, fig. 49).—There is a pair on each of the two petiolar segments and the other five pairs are on the gastral tergites. Each is a circular opening leading into a spherical atrium, which in turn leads into five successive cavities making in all six subdivisions of the atrium. At the base of the last chamber is a closing valve and a lever from which a cylindrical occlusor muscle runs to the sixth chamber. A cylindrical dilator runs from the apex of the lever to a sternal apodeme. Contraction of the occlusor closes the tracheal opening ; the dilator acts as an antagonist to it.

(b) *Lasius fuliginosus* (Latreille) ; (c) *L. niger* (L.)

These two species are dealt with together as no important differences were found.

First thoracic spiracle (Pl. IX, figs. 50, 51).—This lies concealed under the pronotal lobe which is feebly sclerotised and bears long hairs. The spiracular opening is broadly oval and surrounded by a peritreme which gives rise to two membranous flap-like lids situated at a lower level than the integument. The anterior lid remains external to the posterior one ; an acicular muscle is attached to them. The spiracular trachea is irregular in diameter and widens as it leaves the spiracle. Contraction of the muscle pulls the lids over one another to close the spiracle ; the parts are sufficiently elastic to open when the muscle is relaxed. The mechanism described above occurs in males, females and workers.

Second thoracic spiracle (Pl. IX, figs. 52, 53).—This is visible externally, lying in a small triangular sclerite between the mesepimeron and the metapleuron. The external opening has a distinct circular peritreme and leads into a spacious atrium lined with long outwardly projecting hairs. The atrium leads in turn into a small thin-walled cavity, surrounded by a strong sclerotised calliper, to the dorsal side of which a fan-shaped occlusor muscle is attached, arising on the ventroposterior edge of the triangular sclerite referred to above. Contraction of the muscle turns the calliper and closes the spiracle by bringing the membranous walls close to each other ; opening is effected by the elasticity of the parts.

Propodeal spiracle (Pl. IX, fig. 54).—The external opening is crescentic and there is a sclerotised peritreme and a large, shallow, divided atrium, which gives rise ventrally to an elongate lever. A cylindrical occlusor muscle runs between the lever and a notch on the atrial wall. The dilator muscle runs from the tip of the lever ventrally and caudally. Contraction of the occlusor muscle closes the tracheal opening by pushing the elastic closing valve to the opposite side. The spiracle opens by the contraction of the dilator and relaxation of the occlusor.

Gastral spiracles (Pl. IX, fig. 55).—There is a pair on the pedicel and the remaining six pairs are on the sides of the gastral tergites. Each has a roughly elliptical opening leading into a shallow primary atrium which again opens into a large secondary one. Both atria have internally long outwardly directed hairs ; the second gives off a small hook-like lever. The cylindrical occlusor muscle lies between the lever and a notch formed by the two inclined atrial chambers. The dilator takes its origin on a sternal apodeme and inserts on the

lever. Contraction of the occlusor closes the tracheal opening, while the dilator acts as an antagonist to it.

(d) *Formica fusca* L.

First thoracic spiracle (Pl. IX, figs. 56, 57).—There is a freely exposed circular opening posterior to the pronotum. This opening leads into an atrium which is produced into a closing valve and two knobs, one dorsal and the other ventral. An acicular occlusor muscle is attached by means of an elastic apodeme to both the knobs. Contraction of the muscle presses the closing valve against the opposing side to close the tracheal opening: owing to elasticity of the structure relaxation of the muscle allows the spiracle to open.

Second thoracic spiracle (Pl. IX, fig. 58).—Each is a freely exposed, roughly oval opening near the posterior edge of the mesepimeron. There is a well developed atrium and the tracheal opening is partially covered by a closing valve produced by the invagination of the atrial wall. A fan-shaped occlusor muscle runs from the closing valve to its origin on an internal arched sclerotised ridge of the mesepimeron. Contraction of the muscle pulls the closing valve against the tracheal opening to close the spiracle, which opens owing to the elasticity of the parts when the muscle relaxes.

Propodeal spiracle (Pl. X, fig. 60).—This is a freely exposed oval opening on the propodeum and leads into an enormous atrium, the internal walls of which bear outwardly directed hairs. The atrium is produced into two levers, between which the closing valve lies vertical to the axis of the body. A cylindrical occlusor muscle is inserted between the apices of these levers and a similar dilator runs from the smaller lever ventrally and caudally. Contraction of the former closes the tracheal opening.

Gastral spiracles (Pl. X, fig. 59).—Each is a circular opening leading into a small primary atrium which communicates with an enormous secondary one, the walls of which carry outwardly directed hairs. A small lever and the tracheal opening arise from the base of the secondary atrium. The cylindrical occlusor and dilator muscles are inserted on the apex of the lever, the former arising from the atrium while the latter takes its origin on the anterior tergal ridge. The spiracular trachea is narrow at the tracheal opening, one side of which has a closing valve with lever, and widens as it leaves it. Contraction of the occlusor muscle will close the tracheal orifice, the dilator acting as its antagonist.

Pompiloidea

(18) *Pompilidae*

There are two thoracic, one propodeal and seven gastral pairs of spiracles.

(a) *Priocnemis exaltatus* (Fabricius)

First thoracic spiracle (Pl. X, fig. 61).—This lies concealed beneath the posterior lobe of the pronotum. There is an approximately oval opening with a thin peritreme in the segmental membrane between the pronotum and mesepisternum. The peritreme opens into a shallow atrium with thin walls, the membranous flaps, at the base of which is the spiracular trachea. An acicular occlusor muscle is attached to the dorsal side of the atrium. Contraction

of the muscle brings the membranous flaps against each other, thus closing the tracheal opening ; relaxation of the muscle allows the spiracle to re-open.

Second thoracic spiracle (Pl. X, fig. 62).—This lies in the membrane above the mesepimeron and metapleuron and is partially concealed by the irregular sclerite already referred to as the collar of the spiracle. The opening is surrounded by a well developed peritreme and leads into a shallow atrium with thin membranous walls, on the dorsal side of which is a small plate. From the plate a fan-shaped occlusor muscle runs to the posterior side and is attached to the ventral rim of the collar. Contraction of the muscle pulls the anterior side and the posterior wall is tucked under it to close the tracheal opening. The elasticity of the structures allows the opening to be re-established.

Propodeal spiracle.—This is similar in structure and mechanism to the corresponding spiracles in *Neuroterus* except that the ventral lever is the larger of the two.

Gastral spiracles.—These occur on the sides of the first seven tergites, and are similar to the corresponding spiracles in *Neuroterus* except that the dorsal lever is replaced by a manubrium and the dilator arises from the sternal apodeme.

(b) *Pompilus plumbeus* Fabricius

First thoracic spiracle.—This is similar to the corresponding spiracle in *Priocnemis* except that the atrium is shallow and the membranous walls act as internal lids.

Second thoracic spiracle (Pl. X, fig. 63).—This is surrounded by a large collar. The peritreme is a conspicuous rim inside the collar and there is a shallow atrium, on the dorsal side of which is a sclerotised bar or calliper to which is attached a fan-shaped occlusor muscle. The muscle arises on the posteroventral edge of the collar and its contraction brings the membranous atrial walls close together to close the spiracle ; elasticity of the structure allows the spiracle to open when the occlusor relaxes.

Propodeal and gastral spiracles.—These are like the corresponding spiracles in *Priocnemis*.

(c) *Anoplius nigerrimus* (Scopoli)

First thoracic spiracle.—The oval opening, with a distinct peritreme, leads into an atrium which is provided with thin membranous walls and opens basally into the spiracular trachea. An acicular occlusor muscle is inserted at the ventral side of the base of the atrium and takes its origin from the posterior wall of the pronotum. The effect of the contraction of this muscle is to bring the closing valves together and so close the tracheal opening. Opening is effected by the elasticity of the structure.

Second thoracic spiracle.—Each has a conspicuous peritreme surrounded by a collar and leading into a shallow atrium, to the dorsal side of which is a sclerotic calliper on which a fan-shaped occlusor muscle is attached. The muscle is inserted on the posteroventral side of the horseshoe-shaped sclerotic ridge formed around the spiracle. Contraction of the muscle brings the two flexible sides together to close the tracheal opening. The parts are sufficiently elastic to allow the spiracle to re-open when the occlusor muscle relaxes.

Propodeal and gastral spiracles.—These resemble *Priocnemis*.

(d) *Ceropales maculata* (Fabricius)

First thoracic spiracle.—The structure and regulatory mechanism is as described for the corresponding spiracle in *Priocnemis*.

Second thoracic spiracle (Pl. X, fig. 64).—Each has a well developed peritreme, the anterior side of which is fused with the collar. The atrium is shallow and has at its base an irregular sclerotised calliper surrounding the entire tracheal opening. To the anterior edge of the calliper is attached a fan-shaped occlusor muscle which arises from the posteroventral edge of the calliper which is fused with the corresponding edge of the collar. Contraction of the muscle pulls the anterior rim of the calliper to close the tracheal opening.

Propodeal and gastral spiracles.—These do not show any marked differences from the corresponding spiracles in *Priocnemis*.

Vespoidea

(19) *Vespidae*

There are two thoracic, one propodeal and seven gastral pairs of spiracles.

(a) *Vespula germanica* (Fabricius)

First thoracic spiracle.—This is similar to the corresponding spiracles of *Vespula pennsylvanica* (Sauss.), described by Duncan (1939).

Second thoracic spiracle (Pl. X, fig. 65).—This lies in the membrane below the base of the hind wing and just above the mesepimeron and metapleuron. It is covered by an irregularly triangular sclerite (*C*) which Duncan (1939) referred to as the peritreme. Comparison with other Hymenoptera suggests that this sclerite is really what I have called the collar, and that the true peritreme (*P*) of *Vespula* forms a narrow but conspicuous ring around the spiracular opening. The collar is highly sclerotised and its basal corners are curved inwards to embrace the spiracular opening. The latter is partly closed by the membranous operculum (*OP*) which arises from the peritreme.

Propodeal spiracle.—The spiracular opening is an elongate oval aperture situated dorsolaterally on the propodeum. It is surrounded by a simple narrow peritreme within which is a shallow atrium. The base of the atrium opens into a trachea and around the latter opening the cuticle is more sclerotised to form an anterior rigid internal lip (" Bow " of Duncan, 1939) and a posterior flexible closing valve. Arising ventrally in the region where the atrium passes into the closing valve is a conspicuous ventral lever. There is no dorsal lever as described by Duncan (1939) for *Vespula pennsylvanica*. A cylindrical occlusor muscle runs from the thickened dorsal manubrium to the apex of the ventral lever, while the dilator runs from the apex of the lever ventrally and caudally to the sternum. The mechanism has been already described by Duncan (1939).

Gastral spiracles.—These are similar to the gastral spiracles of *Vespula pennsylvanica* described by Duncan (1939), except for the absence of a dorsal lever.

(b) *Vespa crabro* L.

All spiracles resemble the corresponding spiracles of *Vespula germanica* except for their larger size.

(c) *Ancistrocerus trimarginatus* (Zetterstedt); (d) *A. oviventris* (Wesmael)

These are dealt with together as no important differences were noted.

First thoracic spiracle (Pl. XI, fig. 66).—This is concealed beneath the pubescent lobe of the pronotum and has a well developed thick peritreme from the outer edge of which arises a sclerotised operculum. The latter is heavily sculptured and bears a reticulate pattern; to its ventral side is a small acicular occlusor muscle which runs to the ventral edge of the pronotum. Contraction of the muscle pulls the operculum to close the spiracular opening.

Second thoracic spiracle (Pl. XI, fig. 67).—Each is situated just above the infolded membrane between the mesepimeron and the metapleuron and is partially covered by the collar. There is a circular opening with a distinct peritreme giving rise to a well defined operculum, to the anterior side of which is attached a fan-shaped occlusor muscle. This runs to the base of the thickened rim of the collar. Contraction of the muscle pulls the dorsal lid to close the spiracle; this action recalls the movement of a vertical shutter.

Propodeal spiracle.—This is in most respects similar to the corresponding spiracles in *Vespula*, but differs in possessing two levers.

Gastral spiracles (Pl. XI, fig. 68).—These are situated to the anterior side of the intertergal ridges. Each has an oval opening leading into a well developed atrium which is produced into two levers. Between the levers, and perpendicular to the spiracular opening, lies the tracheal opening, bounded by paired closing valves. The cylindrical occlusor muscle is inserted between the apices of the two levers, while a similarly shaped dilator runs from the ventral lever to a sternal apodeme. Contraction of the occlusor muscle presses the closing valves towards each other, thus constricting the tracheal opening; contraction of the dilator opens the spiracle.

Sphecoidea

(20) *Sphecidae*

There are two thoracic, one propodeal and seven gastral pairs of spiracles.

(a) *Astata boops* (Schrank)

First thoracic spiracle (Pl. XI, fig. 69).—This is concealed beneath the pronotal lobe, the spiracular opening lying in the intersegmental membrane between the prothorax and mesepisternum. There is no distinct peritreme, the opening leading directly to the spiracular trachea which widens on leaving the spiracle. The spiracular opening is covered by a sclerotised plate or operculum, which is attached to the anterior side of the opening. An acicular muscle runs from one arm of the operculum to an apodeme from the anterior wall of the mesepisternum. Its contraction closes the spiracular opening by bringing the operculum down; the elasticity of the parts allows the opening to be re-established.

Second thoracic spiracle (Pl. XI, fig. 70).—This lies between the upper edges of the mesepimeron and metapleuron. The external opening is surrounded by a collar and the well defined peritreme is produced into two membranous flaps, at the base of which is an elastic plate to which a fan-shaped occlusor muscle is attached. The muscle arises from the ventral rim of the collar and its contraction brings the two flaps together.

Propodeal and gastral spiracles.—In all important respects these resemble the corresponding spiracles of *Vespula germanica*.

(b) *Trypoxylon clavicerum* (Lepeletier)

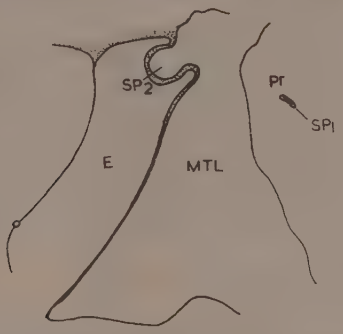
First and second thoracic spiracles.—These resemble the corresponding spiracles in *Astata*.

Propodeal and abdominal spiracles.—These are similar in structure and mechanism to the corresponding spiracles in *Astata*, except that *Trypoxylon* has two levers on the propodeum.

(c) *Podalonia viatica* (L.)

First thoracic spiracle.—This is like the corresponding spiracles in *Astata*.

Second thoracic spiracle (Pl. XI, fig. 71).—This is concealed and its precise location needs discussion. The dorsal and posterior edges of the mesepimeron



TEXT-FIG. 4.—*Podalonia viatica* (L.). Thoracic sclerites around the spiracle, lateral view.

enclose a deep emargination, into which the metapleuron projects as a pubescent lobe (text-fig. 4). The spiracle lies concealed beneath this lobe. The spiracular opening is surrounded by a conspicuous peritreme and leads immediately into the spiracular trachea. The opening is covered by an operculum, to which is attached a fan-shaped occlusor muscle arising from the ventral edge of the metapleural lobe. Contraction of this muscle pulls down the operculum and closes the spiracular opening.

Propodeal and gastral spiracles.—These are similar in structure and mechanism to the corresponding ones in *Trypoxylon*.

(d) *Cemonus lethifer* (Shuckard)

First and second thoracic spiracles.—These resemble the corresponding ones in *Astata*.

Propodeal and abdominal spiracles.—These resemble the corresponding spiracles in *Astata* and *Trypoxylon* respectively.

(e) *Oxybelus uniglumis* (L.)

All the spiracles agree in structure with the corresponding spiracles in *Astata*, except that the gastral spiracles are similar to those of *Trypoxylon*.

(f) *Crabro cribrarius* (L.)

First and second thoracic spiracles.—These are similar to the corresponding spiracles in *Astata* and *Podalonia* respectively.

Propodeal and gastral spiracles (Pl. XI, fig. 72).—These are similar to those of *Astata* except that the occlusor muscle lies between the lever and the anterior wall, there being no manubrium.

(g) *Hoplocrabro quadrimaculatus* (Fabricius)

First thoracic spiracle (Pl. XI, fig. 73).—This is similar to the first thoracic spiracle of *Astata*.

Second thoracic spiracle (Pl. XII, fig. 74).—This lies in the membrane beneath a roughly triangular sclerotic extension of the mesepimeron and below the hind wing. The spiracular opening is surrounded by a well defined peritreme from which arises an operculum. At the place of its attachment the operculum has a short arm on which is inserted a fan-shaped occlusor muscle. The muscle arises from a flange and its contraction lowers the operculum to close the spiracular opening; the elasticity of the structure allows the opening to be re-established.

Propodeal and gastral spiracles.—These are similar to those of *Astata*.

(h) *Mellinus arvensis* (L.)

All spiracles are similar to those of *Astata*.

(i) *Cerceris rybyensis* (L.); (j) *C. arenaria* (L.); (k) *C. quinquefasciata* (Rossi)

All spiracles resemble the corresponding ones in *Astata*.

Apoidea

There are two thoracic, one propodeal and seven gastral pairs of spiracles.

(21) *Colletidae*

(a) *Colletes similis* Schenck

First thoracic spiracle (Pl. XII, fig. 75).—This lies concealed beneath a pubescent lobe-like extension of the posterodorsal corner of the pronotum. When the lobe is lifted the spiracle is seen lying in the membrane between the pro- and mesothorax as a simple, irregularly oval aperture, the long axis of which is at right angles to the axis of the body. It is half covered by an irregularly shaped plate or operculum, which is curved and shallow and attached laterally to the membrane around the spiracular opening. From the latero-dorsal end of the operculum an acicular occlusor muscle runs to the posterior wall of the pronotum. When this muscle contracts the operculum is moved down to close the spiracle.

Second thoracic spiracle (Pl. XII, fig. 76).—This lies in the membrane immediately above the mesepimeron and metapleuron and below the insertion of the hind wings. The approximately circular opening of the trachea is surrounded by a thickened, sclerotised peritreme and partly covered by a hinged operculum attached to the peritreme by its dorsal edge; the ventral edge of the operculum forms a free flap. Around the peritreme is an irregularly shaped, less heavily sclerotised zone which forms a shallow bowl-like region—the spiracular depression. Bounding the depression is a strongly sclerotised rim which is continuous internally with a well developed flange. The latter is strongly developed posteriorly and forms a much smaller projection anteriorly. The trachea leaving the peritreme thus passes through the curved flange. Running from the posterior part of the opercular hinge to the adjacent region of the inner surface of the flange is the fan-shaped occlusor muscle. Its contraction lowers the operculum and so helps to close the spiracle.

It may be noted that previous authors (*e.g.* Duncan, 1939; Michener, 1944) refer to the rim of the collar as the peritreme. For reasons which will be apparent from the present section and that on the Vespoidea, the above nomenclature is preferable.

Propodeal spiracle (Pl. XII, fig. 77).—Except for minor structural differences this does not differ from the corresponding spiracles in *Astata*.

Gastral spiracles.—These lie on the sides of the abdominal tergites. The external opening is a narrow slit leading to a shallow atrium the walls of which have short hairs internally, and spiral cuticular thickenings externally. The atrium is produced into two large levers between which lies the occlusor muscle, the contraction of which closes the tracheal opening by bringing the two valves closer to each other. The dilator muscle runs between the ventral lever and a sternal apodeme.

(b) *Prosopis* sp.

First thoracic spiracle.—As in *Colletes*, this spiracle is concealed by the pronotal lobe. From the sclerotised peritreme arises a movable operculum, to the dorsal edge of which is attached a slender acicular occlusor muscle running to the posterior wall of the pronotum. Contraction of the muscle moves the dorsal operculum downwards and the ventral part of the peritreme is also tucked beneath it. The closing mechanism in this spiracle recalls the movement of the lids.

The remaining spiracles are essentially similar to the corresponding spiracles of *Colletes*.

(22) *Halictidae*

(a) *Halictus leucozonius* (Schranck)

First thoracic spiracle.—This is similar in structure and function to the corresponding spiracle of *Prosopis*, except that the occlusor muscle is attached to the dorsal operculum by means of a long elastic tendon-like apodeme. The other attachment of the occlusor muscle is to a well marked ridge of the anterior wall of the mesepisternum.

Second thoracic spiracles.—These agree in detail with the corresponding spiracles in *Colletes*.

Propodeal spiracle and gastral spiracles.—These are as described above for the corresponding spiracles of *Prosopis*.

(b) *Sphecodes* sp.

First thoracic spiracle. As in *Prosopis*.

Second thoracic spiracle (Pl. XII, fig. 78).—The position of this spiracle is the same as in *Colletes*. The sclerotised peritreme is produced into membranous elastic flaps (not shown in fig. 78), and a short tubular region connects the spiracular trachea with the peritreme. The flange is not well developed but from it arises a fan-shaped occlusor muscle which runs to the ventral side of the tubular region. The contraction of this muscle transforms the originally circular aperture into an elongate slit, the opposing walls of which are almost in contact, and so virtually closes the aperture.

Propodeal spiracle and gastral spiracles.—These are similar in structure and mechanism to those of *Colletes* and *Prosopis* respectively.

(23) *Andrenidae*

(a) *Andrena flavipes* Panzer

First and second thoracic spiracles.—These resemble in structure and mechanism those of *Prosopis* and *Colletes* respectively.

Propodeal and gastral spiracles.—These are similar to the corresponding spiracles of *Prosopis*.

(b) *Panurgus banksianus* (Kirby)

First thoracic spiracle (Pl. XII, fig. 79).—In this species the pronotal lobe seems to be firmly pressed against the mesepisternum and there is thus a deep semicircular groove on the margin of the pronotal wall. The spiracular opening lies near the base of the vestibule formed by the pubescent pronotal lobe and the depressed mesepisternum, and is mostly surrounded by membrane between the two sclerites. The tracheal opening is small and leads to a short space bounded by flexible membranous flaps. These in turn join the spiracular trachea, which enlarges on leaving the spiracular opening. To the dorsal side of the membranous wall is attached a long tendon-like apodeme with an acicular occlusor muscle which runs ventrally to an apodeme of the mesepisternum; its contraction moves the membranous flap to the ventral side, thus closing the spiracle. The spiracle is interesting in two respects: the air first passes through a cavity, the vestibule, and the closing mechanism is situated at the base of the vestibule.

The remaining spiracles are similar to the corresponding spiracles in *Colletes*.

(24) *Megachilidae*

(a) *Megachile argentata* (Fabricius)

First thoracic spiracle.—This is similar to the first thoracic spiracle of *Colletes* except that the spiracular opening is at an angle of 45° to that of the body and the occlusor muscle is attached to an apodeme of the mesepisternum.

Second thoracic spiracle (Pl. XII, fig. 80).—This has some similarities to the corresponding spiracle in both *Nomada* and *Colletes*. It is half concealed by the collar externally and the opening is a distinct sclerotised oval ring covered

by an anteriorly hinged operculum from which a fan-shaped occlusor muscle runs to the sclerotic extension of the wall of the peritreme, as in *Nomada*. Contraction of the muscle lowers the operculum and so occludes the aperture.

Propodeal and gastral spiracles.—These are similar to those of *Colletes* and *Panurgus* respectively.

(b) *Anthidium manicatum* (L.)

First and second thoracic spiracles.—These are similar to those of *Megachile* and *Sphecodes* respectively.

Propodeal and gastral spiracles.—These agree in structure and mechanism with those of *Prosopis*.

(c) *Stelis aterrima* (Panzer)

First thoracic spiracle.—This is similar in structure and mechanism to *Prosopis*.

Second thoracic spiracle (Pl. XII, figs. 81, 82).—The collar does not surround the spiracular opening but is attached to its anterior margin. Anteriorly the peritreme is strongly sclerotised and fused with the collar, while its posterior margin is less strongly sclerotised. Between the peritreme and the spiracular trachea is a short membranous band, as in *Sphecodes*, but in *Stelis* the muscle runs from the posterior, more flexible, wall to the ventral part of the rim of the collar. Contraction of the muscle deforms the aperture to close it.

Propodeal spiracle.—This is very similar to the corresponding spiracles in *Prosopis*.

Gastral spiracles.—Each has an oval opening leading into a deep outer atrium, the thick walls of which bear heavy external cuticular thickenings; internally they are provided with short hairs pointing towards the spiracular opening. The outer atrium leads into a short inner atrium which has smooth walls and lies at right angles to the outer one. The inner atrium is produced into two small levers of equal size. The occlusor and dilator muscles and the mechanism of closing resemble that in the gastral spiracle of *Colletes*.

(d) *Osmia coerulescens* (L.)

First and second thoracic spiracles.—These resemble those of *Colletes* and *Stelis* respectively.

Propodeal and gastral spiracles.—These are similar to those of *Prosopis* and *Stelis* respectively.

(25) *Apidae*

(a) *Anthophora bimaculata* (Panzer)

First and second thoracic spiracles.—These are similar in structure and mechanism to those of *Panurgus* and *Stelis* respectively.

Propodeal and gastral spiracles.—These resemble those of *Prosopis* and *Panurgus* respectively.

(b) *Nomada rufipes* Fabricius

First thoracic spiracle.—This is similar in structure and mechanism to the corresponding spiracle of *Colletes*.

Second thoracic spiracle.—The sclerotised circular opening is not surrounded by the collar; instead, the collar holds the external rim of the peritreme, as in *Vespula*. The external opening leads to a small chamber-like atrium, the walls of which are membranous and flexible basally; from them a short fan-shaped occlusor muscle runs to a curved sclerotic outgrowth of the atrial wall. This structure is functionally analogous to the "flange" mentioned in the description of the second thoracic spiracle of *Colletes*, though its origin is atrial and not from the rim of the spiracular depression, which in *Nomada* remains uninflected. It is not to be confused with the lever or similar movable part of the spiracle but simply provides a site of attachment for the occlusor muscle. Contraction of the muscle brings the closing valves together, thus occluding the tracheal orifice.

Propodeal and gastral spiracles.—These are similar to the corresponding spiracles in *Prosopis* and *Panurgus* respectively.

(c) *Bombus agrorum* (Fabricius)

First thoracic spiracle.—As in *Colletes*, except that the occlusor muscle is larger and is attached by an elongate tendon-like apodeme to the operculum. The muscle runs ventrally to an apodeme of the mesepisternum.

Second thoracic spiracle.—This is similar in structure and mechanism to the corresponding spiracle in *Anthophora*.

Propodeal and gastral spiracles.—These are like those of *Prosopis*.

V. Discussion

It is convenient here to consider a number of points of general interest.

(1) *General Characters of Hymenoptera*

Certain characteristics, many of them negative ones, found in all species studied are listed below.

First thoracic spiracle: without collar or rigid external lid; levers, manubrium and dilator muscle absent; a single acicular occlusor muscle always present.

Second thoracic spiracle: without levers, manubrium or rigid external lids; dilator muscle and pronotal occlusor sclerite absent; a single fan-shaped occlusor muscle always present.

First abdominal (propodeal) spiracle: always present on side of first tergite (propodeum) and freely exposed; always with a shallow atrium and a closing valve, the occlusor and dilator muscles each single and cylindrical.

Gastral spiracles: with a discrete peritreme and a cylindrical occlusor and dilator.

It is difficult, without comparing this order with other insect orders, to say whether other, more positive, features of all Hymenopteran spiracles exist. This is hardly profitable in the present state of our knowledge but it is hoped that the data in this account will ultimately be supplemented by similar extensive investigations of other orders.

(2) *Types of Closing Mechanism*

It is now possible to propose a classification of the spiracles of Hymenoptera based on the various types of closing mechanism. Each type is defined and examples of its occurrence indicated.

(a) *External closing mechanisms*

These involve movement of structures which close the external spiracular opening and are usually, though not always, developed from the peritreme. An atrium is not generally recognisable. There are four kinds :

(i) *Outer peritremal lids.*—Here there are one or two outwardly convex, semimembranous lids arising from the peritreme and controlled solely by a single occlusor muscle working against the elastic circumperitremal region. One of the lids may be larger and more readily movable. Closure occurs in a manner recalling the movement of an eyelid and takes place against the peritreme when only one lid is present, or against the less movable or fixed lid where there are two. This occurs in the two thoracic spiracles of all Symphyta, and the anterior thoracic spiracle of Bethyloidea.

(ii) *Concealed operculum.*—In this type the spiracular opening is concealed by a thoracic process and may be closed by the movement of a single, outwardly convex, sclerotised operculum attached by an elastic hinge to the peritremal region. The movement of this operculum is never like that described for type (i) but varies according to the site of attachment of a single occlusor muscle and may be compared with the movement of either (*a*) a hinged door (lateral attachment) or (*b*) the lid of a box (internal attachment). It is found in one or both of the thoracic spiracles of at least some members of Apoidea, Sphecoidea, Vespoidea, Chalcidoidea and Ichneumonoidea.

(iii) *Inner peritremal flaps.*—In this type the closing apparatus consists of two internal inflections of the peritremal region, outwardly concave, which are moved by a single occlusor muscle so as to approach each other near the external spiracular opening, which they then occlude. It is usually found in the second thoracic spiracles of Formicoidea.

(iv) *Pronotal occlusor sclerite.*—Here there is a large heavily sclerotised sculptured sclerite internally, flexibly articulated to the dorsal and posterior wall of the pronotum, thus freeing the spiracular opening from the intersegmental membrane. Its flexible articulation facilitates the closing of the spiracle when pulled down by an occlusor which is attached to it. This type is generally exposed, but concealed in some Braconidae, *e.g.* the first thoracic spiracle of Ichneumonoidea.

(b) *Internal closing mechanisms*

These involve the movement of structures which close the opening of the tracheae into the atrium, the latter structure always being recognisable. There are three types :

(i) *Calliper compression of atrium.*—In this type the basal part of the atrium is folded with a slightly sclerotised ring completely or partially around it. Variations in the structures are too numerous to mention here but are described in the relevant systematic section. The principle involved is a simple one, *viz.*, deformation of the normal circular tracheal opening so as to close it, brought about by a single occlusor muscle. It is of general occurrence in the first thoracic spiracle of Proctotrupoidea and Cynipoidea and of some Formicoidea and Pompiloidea, but in the latter the atrium remains shallow. In the Evanioidea the insertion of the occlusor muscle is between the dorsal pronotal inflection, which is movable, and the ventral pronotal apodeme.

(ii) *Lever-actuated closing valve.*—Though this does not, strictly speaking, involve a valve (*i.e.* a structure permitting flow of fluid in one direction only) the term is firmly established in the literature and its use is continued here. The position of the valve is altered by movements of the levers in such a way as to occlude the atrial cavity as would a sliding door. There may be one or two valves and one or two levers. The occlusor muscle is always antagonised by a dilator. It is found generally in the propodeal spiracles.

(iii) *Direct atrial constriction.*—Here an elastic valve (or valves) near the atrio-tracheal opening is deformed by contraction of an occlusor muscle so that opposing sides are brought closer and the former opening closed. It is found in the gastral spiracles.

(3) *Spiracular Structure in Relation to the Natural Classification of Hymenoptera*

The division of the Hymenoptera into Symphyta and Apocrita is supported by four differences in spiracular structure. Thus all Symphyta studied have :

(i) First thoracic spiracles with one or two external lids.
(ii) Second thoracic spiracles always with two external lids.
(iii) First abdominal spiracles identical with subsequent ones.
(iv) All abdominal spiracles with a tergal dilator muscle.

On the other hand, the Apocrita have the following common features :

(i) First thoracic spiracles with specially differentiated structures (operculum, inner membranous flaps or pronotal occlusor sclerite) in place of lids.
(ii) Second thoracic spiracles with two internal lids.
(iii) First abdominal spiracle (= propodeal) distinguished from remainder by a shallow atrium.
(iv) Propodeal spiracle with sternal dilator ; gastral with tergal or sternal dilator.

While the Symphyta and Apocrita seem readily distinguishable in their spiracular structure, it is quite impossible to find any character which serves to separate a group of Parasitica from an Aculeate group, even when allowance is made for differences of opinion on the precise limits of two such sections. So far as number and arrangement of spiracles is concerned, the Formicoidea, Vespoidea, Pompiloidea, Sphecoidea and Apoidea all retain the primitive complete condition of the Symphyta. The same is true of Ichneumonoidea which, in this respect at least, must be regarded as the most primitive of the parasitic groups. The four remaining parasitic superfamilies and the Bethyloidea are all more or less specialised and if mere number of spiracles lost is taken as a criterion, the Chalcidoidea, Cynipoidea and Evanioidea are most specialised, with the Proctotrupoidea differing widely among themselves in the degree of reduction of gastral spiracles. Some indication of the way in which the major groups of Apocrita resemble and differ from each other in respect of their spiracular structure may be obtained by comparing them on the basis of about 30 characters discussed in the systematic section (pp. 491–514). Table I shows the percentage of characters in which each group resembles any other group. No attempt has been made, in compiling this table, to evaluate

TABLE I.—*Percentage of spiracular characters shared by different Hymenopteran superfamilies*

uperfamily	Ichn.	Evan.	Cynip.	Chalc.	Proct.	Beth.	Form.	Pomp.	Vesp.	Sphec.	Apoid.
eumonoidea .	100	33	52	46	49	36	36	46	69	71	76
nioidea . .	.	100	58	60	33	33	33	48	64	62	51
poidea . .	.	.	100	58	48	45	28	46	49	45	45
cidoidea .	.	.	.	100	50	28	28	45	46	60	61
totrupoidea .	.	.	.	.	100	46	60	46	39	39	32
yloidea .	.	.	.	.	.	100	52	52	51	57	36
nicoidea .	.	.	.	.	.	.	100	54	47	51	43
piloidea .	.	.	.	.	.	.	.	100	78	72	54
oidea . .	.	.	.	.	.	.	.	.	100	71	78
coidea .	.	.	.	.	.	.	.	.	.	100	78
idea .	.	.	.	.	.	.	.	.	.	.	100

the significance of the various characters on which it is based—indeed, such evaluation is so difficult as to be only of questionable value—and it would therefore be unwise to read a phylogenetic significance into all the resemblances in the absence of confirmatory evidence from other anatomical features.

With the above reservations, the following conclusions may be drawn from this table :

(i) The superfamilies of the Parasitica do not show very striking similarities, the most noteworthy being that between the Evanioidea, Cynipoidea and Chalcidoidea.

(ii) There is a high degree of resemblance between the Sphecoidea and Apoidea, thus confirming a relationship long regarded as likely on other grounds.

(iii) The Vespoidea and Pompiloidea also share a high proportion of characters; this is a relationship which reflects the traditional position of the Pompilidae, though the two groups are often regarded as rather distinct by modern authorities (*e.g.* Berland, *in* Grassé, 1951) who have split up the Vespoidea of Ashmead (1900, etc.). As to the Chrysididae, which were also included in the Vespoidea of older authors, spiracular structure provides little indication of their affinities ; they show no more resemblance to the Vespoidea than to three other Aculeate superfamilies.

(iv) The Apoidea and Vespoidea show a much closer similarity than might have been expected—as high (78 per cent.) as that between Apoidea and Sphecoidea. All three, Apoidea, Sphecoidea and Vespoidea, seem more alike than any other association of superfamilies.

(v) The Formicoidea show no outstanding resemblance to any of the other Aculeate superfamilies. Their resemblance to the Proctotrupoidea, though not unusually great, is perhaps a little unexpected. It depends on both groups having an internal closing mechanism in the thoracic spiracles.

In seeking possible resemblances between the aculeate and the parasitic groups it is noteworthy that it is the Vespoidea and Sphecoidea which tend to show the greatest similarity to the Parasitica and this resemblance is, more especially, between these two superfamilies and the Ichneumonoidea.

From a phylogenetic standpoint, it is necessary again to emphasise the serious limitations of the above inferences from spiracular morphology. Many of the characters compared probably arose convergently, as may be suspected from the great variety of conditions found in the Formicoidea, which indicates

something of the evolutionary plasticity of the structures. There is also a very interesting correlation between the thickness of the cuticle in which the spiracles are set and the degree of development of the atrium with its associated structures, including the position of the internal closing mechanism. Thus all the thoracic spiracles set in membrane have an external closing mechanism without an atrium. Prothoracic spiracles set in the sclerotised pronotum (*e.g.*, Proctotrupoidea, Cynipoidea and *Formica*) have a well developed atrium with an internal closing mechanism. Further, in the Proctotrupoidea, *Formica* and *Lasius* the second thoracic spiracle is set in sclerotised cuticle and again has a well developed atrium and internal closing apparatus. In the Symphyta, Chalcidoidea and Cynipoidea the abdominal tergites are relatively thin and the atria markedly shallow. Any increase in the thickness of the tergites is accompanied by an increase in the depth of the atrium. Good examples are found in the Formicoidea ; *Lasius*, with thin abdominal tergites has a single atrium, *Formica* with thicker tergites has two, whereas *Myrmica*, with a still thicker cuticle, has as many as six chambers. In *Lygocerus* the propodeal spiracle has a well developed atrium whereas in *Phaenoserphus* it is relatively shallow. In Evanioidea the gastral spiracles of *Gasteruption* have a shallow atrium whereas in *Zeuxevania* there is a deep and spacious one. Conversely in Chrysididae, which provide the sole example in which the gastral spiracles are set in tergites or laterotergites, the atria show degrees of development depending on the thickness of the sclerite in which they are set.

While the functional significance of this correlation is not clear—any interpretation in terms of water conservation would be quite speculative—there is no doubt of its existence and probable importance in any attempts to use spiracular features in a phylogenetic connection. Incidentally, the correlation serves to explain why thoracic spiracles generally have an external closing mechanism while the abdominal ones have an internal apparatus, and it also accounts for the few exceptions to this rule.

Comparison with such data as are available for other orders of insects shows that the acicular occlusor muscle of the Hymenopteran prothoracic spiracle seems not to occur elsewhere, but that each of the other general features of the Hymenoptera occurs in at least one order. Curiously enough, the spiracles of the Megalopteran *Sialis* differ appreciably from those of the Hymenoptera ; among the other Endopterygotes, the Mecoptera are very similar in many features to the Hymenoptera, especially to the Symphyta. Until more is known of the comparative morphology of the spiracles in other orders, however, our knowledge of their structure and function in the Hymenoptera can hardly be used to suggest the affinities of the group.

VI. Summary

An illustrated account is given of the comparative morphology of the spiracles of 75 species of adult Hymenoptera. Two main types of closing mechanism are recognised in the order—external and internal. Although both types occur in the thoracic spiracles the latter only is found in the abdominal region. The external type involves movement of lids, a pronotal occlusor sclerite, and an operculum or membranous flaps, and examples of these various subdivisions are cited. The internal closing type includes three kinds, possessing either

(*a*) callipers, (*b*) lever actuated flap-valves or (*c*) lever compression of the atrio-tracheal junction. The spiracles can also be classified according to the shape of their muscles. Three types are recognised, (1) an acicular occlusor of the first thoracic, (2) a fan-shaped occlusor of the second thoracic and, finally, (3) a cylindrical or parallel type found in the abdominal spiracles. Some possible phylogenetic implications of these findings are pointed out, though effects of convergence should be borne in mind. An interesting correlation seems to exist between the thickness of the cuticle in which the spiracles are set and the degree of development of the atria.

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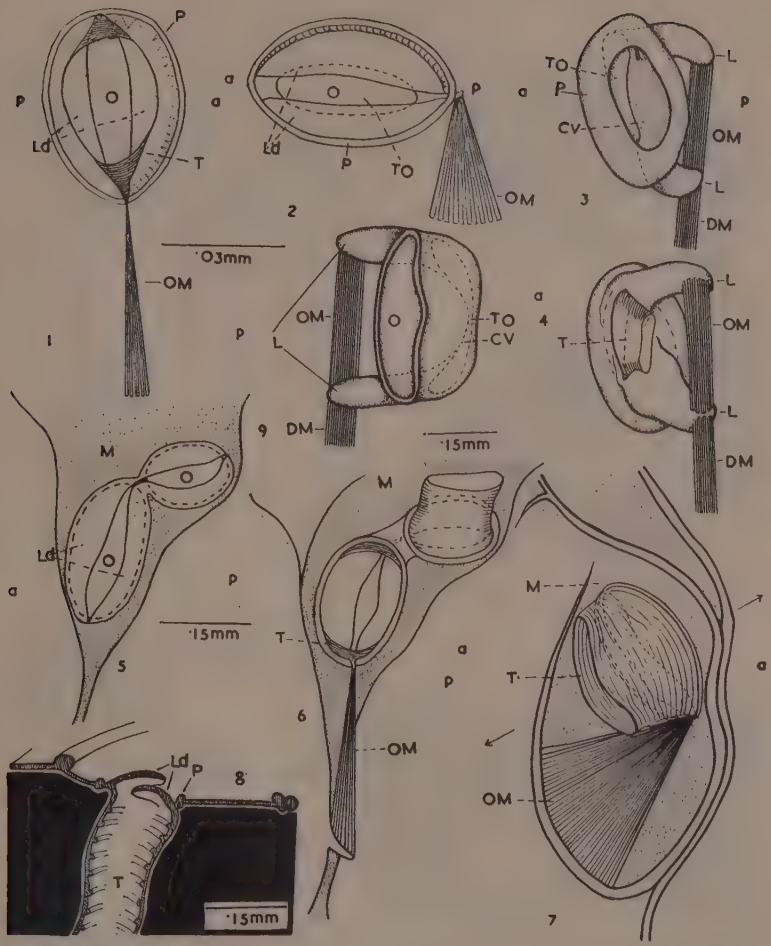
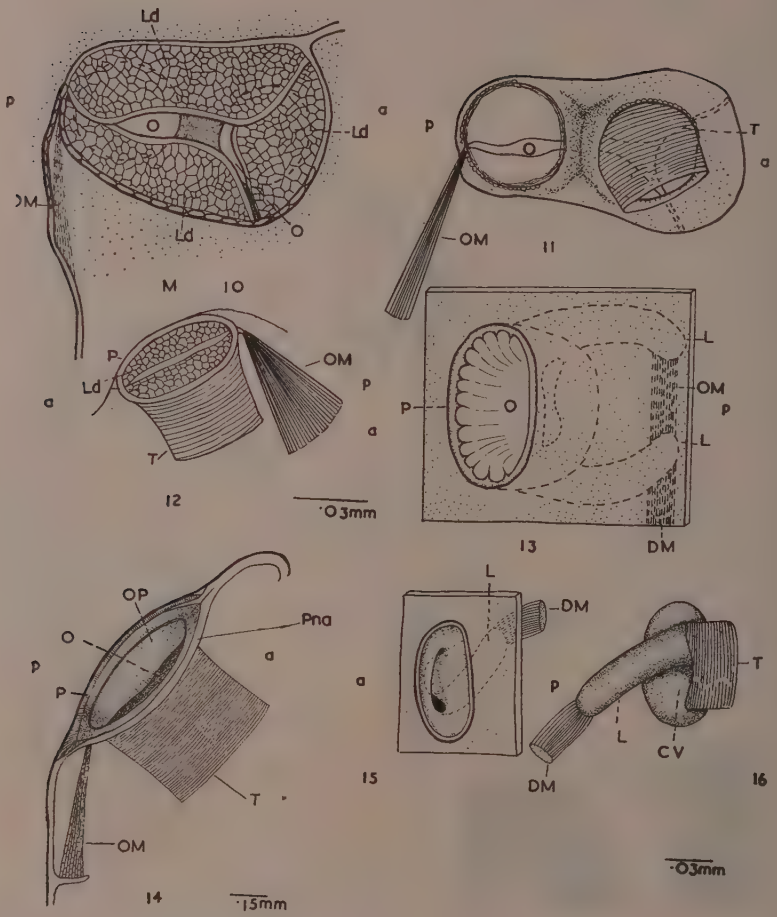
Explanation of Lettering to plates

A, atrium.
a, anterior.
A_2–A_6, number of subdivisions of the atrium.
AL, anterior lip.
C, collar.
CL, calliper.
Cp, circumperitremal area.
CV, closing valve.
DM, dilator muscle.
E, epimeron.
F, flange.
G, groove.
l, dorsal pronotal inflection.
L, lever.
Ld, lid.
M, membrane.
MTL, metapleuron.
MTLO, metapleural lobe.
O, spiracular opening.
OM, occlusor muscle.
OP, operculum.
P, peritreme.
p, posterior.
PE, elastic plate.
Pl, posterior lip.
Pn, pronotum.
Pna, pronotal arch.
Pr, propodeum.
PS, pronotal occlusor sclerite.
R, ring.
Ri, rim.
S, episternum.
*Sp*1–2, spiracles.
T, trachea.
TE, episternal paraptera (Snodgrass, 1910).
TO, tracheal opening.
U, manubrium.
V, vestibule.



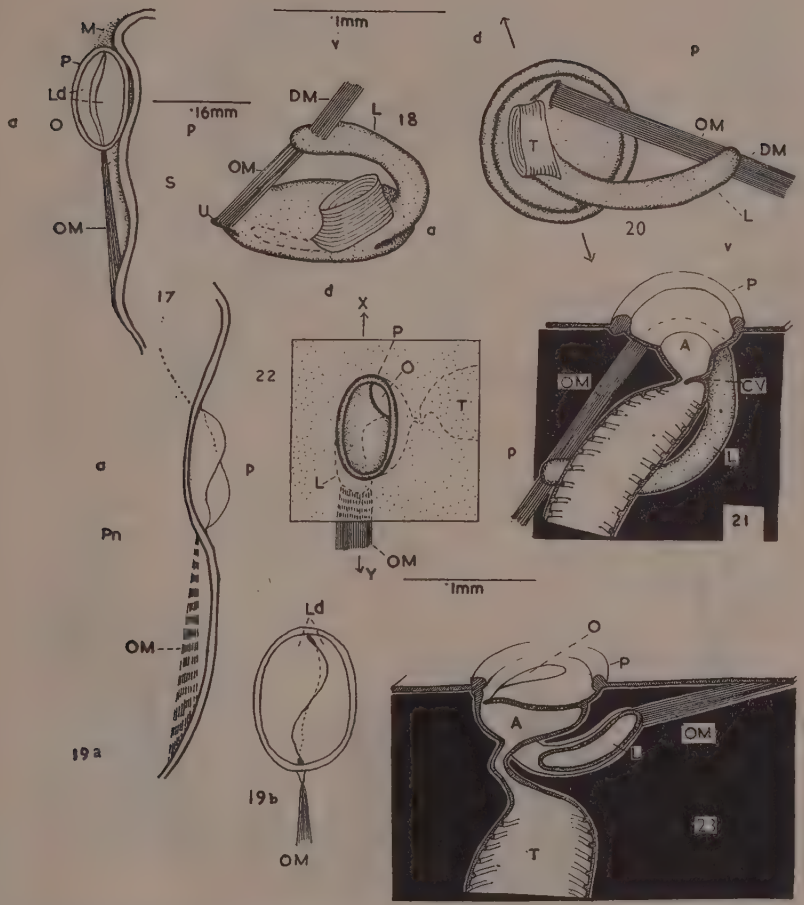
FIGS. 1–4.—*Xyela julii* (Brébisson): (1) Anterior thoracic spiracle, internal view; (2) posterior thoracic spiracle, external view; (3) third abdominal spiracle, external view; (4) fifth abdominal spiracle, internal view.

FIGS. 5–8.—*Sirex juvencus* (L.): (5) Anterior thoracic spiracle, external view; (6) the same, internal view; (7) posterior thoracic spiracle, internal view; (8) the same, schematic sectional view in the plane of the arrow; (9) abdominal spiracle, external view.



FIGS. 10–13.—*Cephus cultratus* Eversmann: (10) Anterior thoracic spiracle, external view; (11) the same, internal view; (12) posterior thoracic spiracle, internal side view; (13) fourth abdominal spiracle, external view.

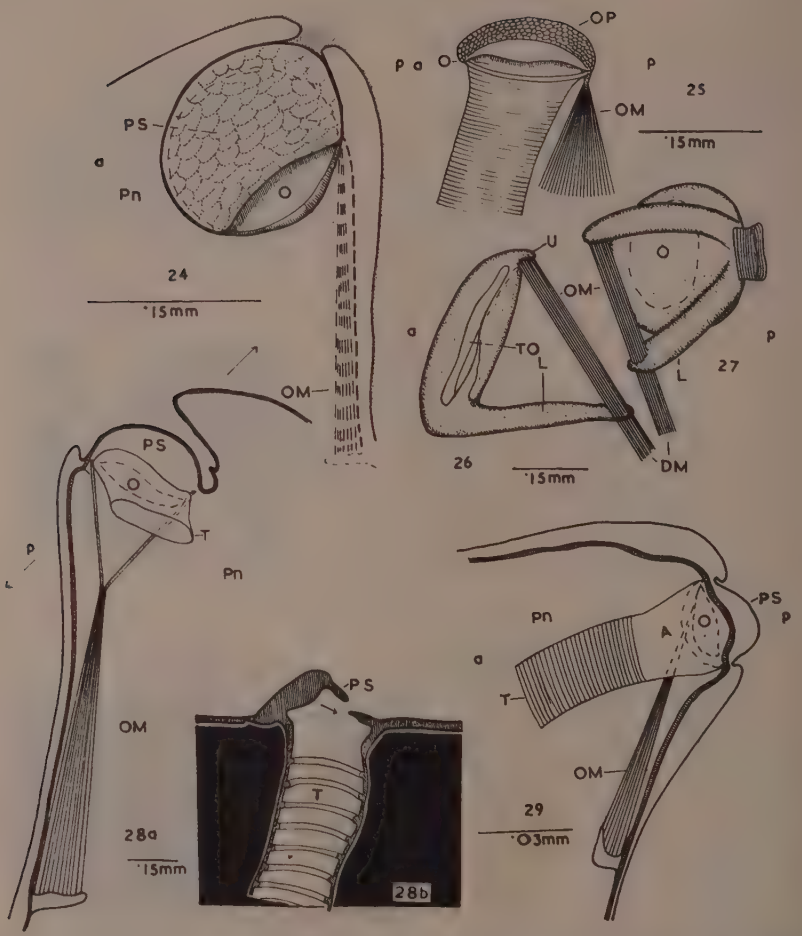
FIGS. 14–16.—*Diprion pini* (L.): (14) Anterior thoracic spiracle, internal side view; (15) fifth abdominal spiracle, external view; (16) the same, internal view.



Figs. 17–18.—*Tenthredo arcuata* Forster : (17) Anterior thoracic spiracle, external view ; (18) abdominal spiracle, internal view.

Figs. 19–21.—*Dolerus niger* (L.): (19) (*a*) External side view of pronotum; anterior thoracic spiracle, external view ; (*b*) the same, frontal view ; (20) third abdominal spiracle, internal view ; (21) the same, schematic sectional view in the plane of the arrow.

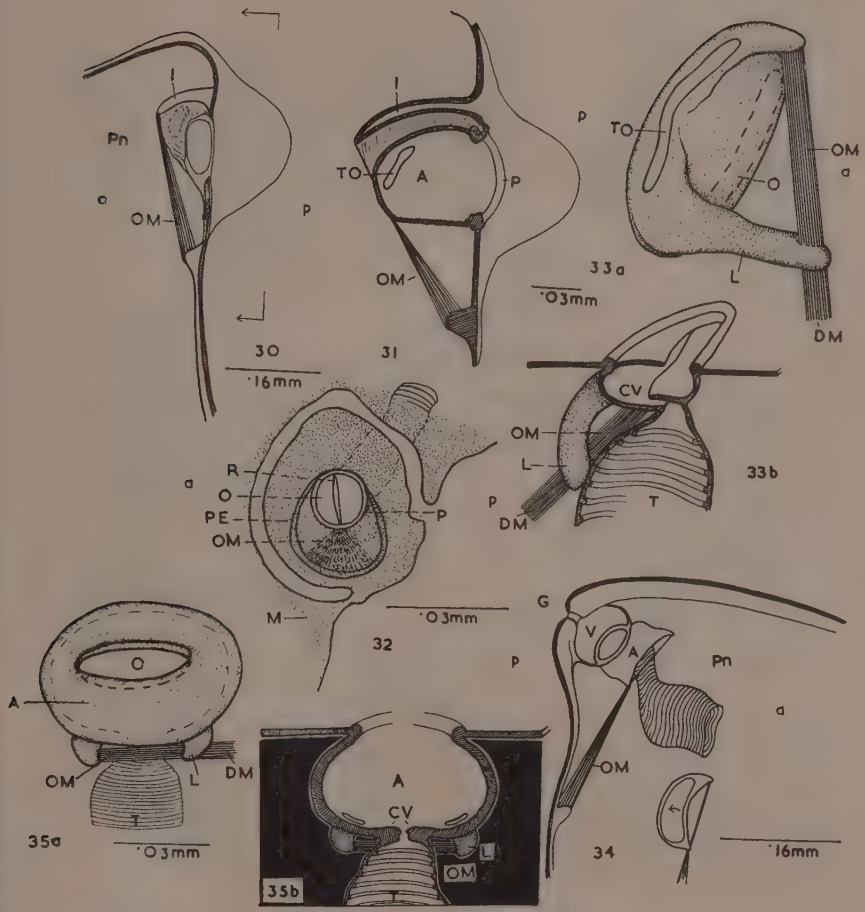
Figs. 22–23.—*Taxonus agrorum* (Fallén): (22) Third abdominal spiracle, external view; (23) diagrammatic sectional view along X–Y.



FIGS. 24–27.—*Amblyteles* sp. : (24) Anterior thoracic spiracle, external view ; (25) posterior thoracic spiracle, internal side view ; (26) propodeal spiracle, internal view ; (27) third gastral spiracle, internal view.

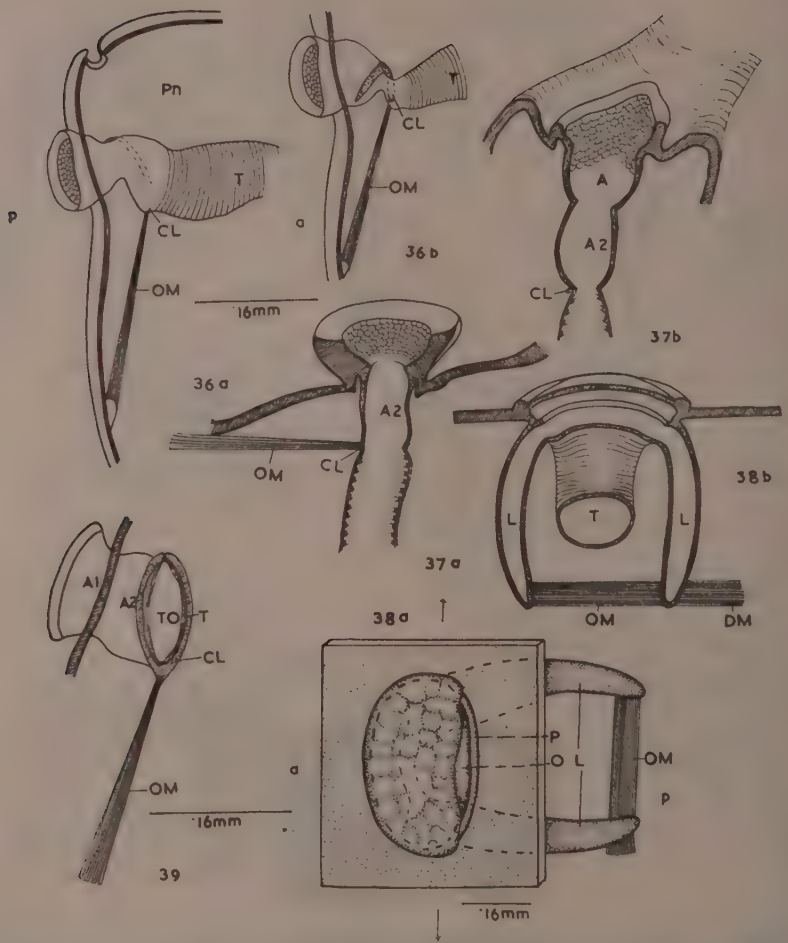
FIG. 28.—*Pimpla instigator* (Fabricius): Anterior thoracic spiracle, (*a*) internal side view ; (*b*) schematic sectional view in the plane of the the arrow.

Fig. 29.—*Brachistes* sp. : Anterior thoracic spiracle, internal side view.



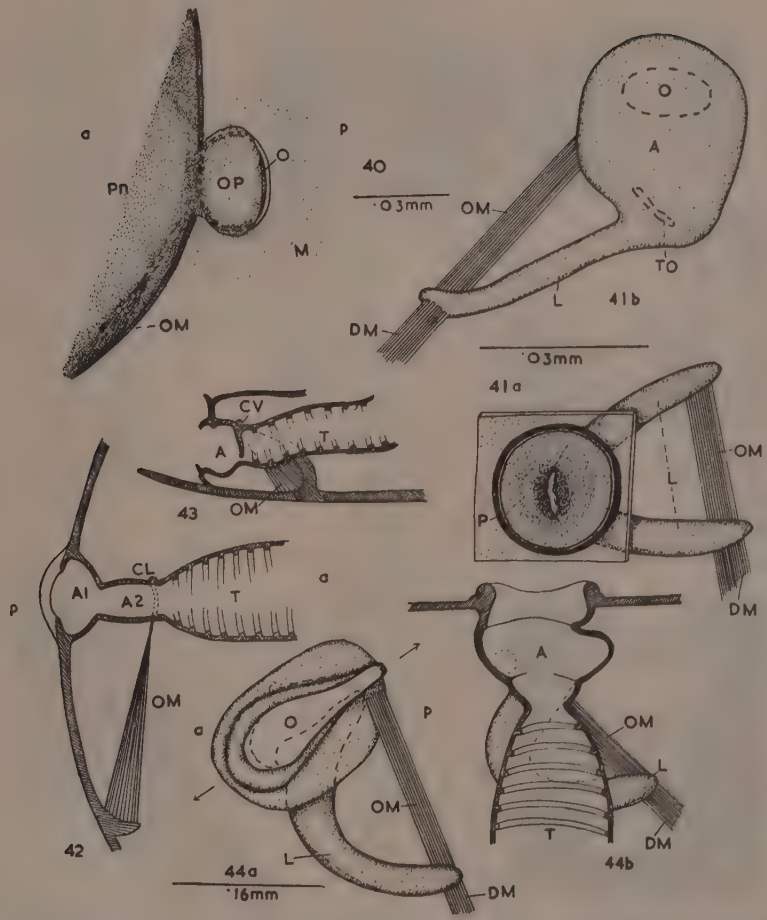
FIGS. 30–33.—*Gasteruption assectator* (L.): (30) Anterior thoracic spiracle, internal side view; (31) the same, schematic sectional view in the plane indicated; (32) posterior thoracic spiracle, external view; (33) propodeal spiracle, (*a*) internal view; (*b*) sectional view.

FIGS. 34–35.—*Zeuxevania splendidula* (Costa): (34) Anterior thoracic spiracle, internal side view; (35) gastral spiracle, (*a*) internal side view; (*b*) schematic sectional view.



FIGS. 36–38.—*Neuroterus kollari* (Hartig): (36) Anterior thoracic spiracle, (*a*) internal side view; (*b*) dorsal view (half closed); (37) (*a*) and (*b*) the same, schematic sectional view (38) propodeal spiracle, (*a*) external view; (*b*) diagrammatic sectional view in the plane of the arrow.

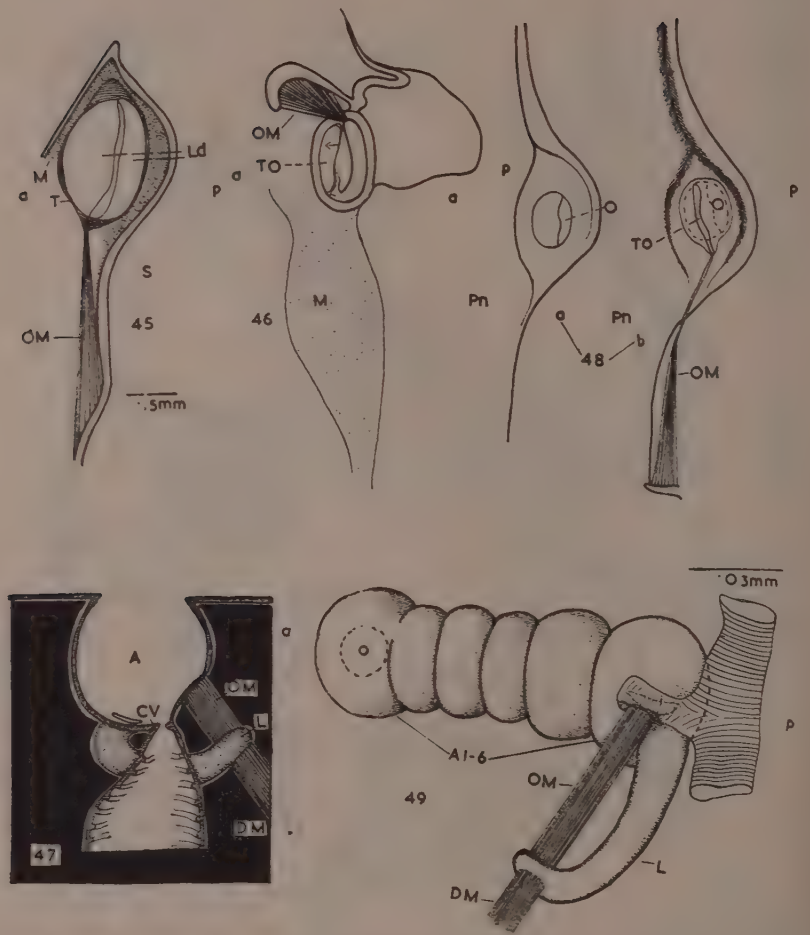
FIG. 39.—*Rhodites rosae* (L.): Anterior thoracic spiracle, internal side view (open).



FIGS. 40–41 (*a*).—*Mormoniella vitripennis* (Walker): (40) Anterior thoracic spiracle, external side view; (41) gastral spiracle, external view.

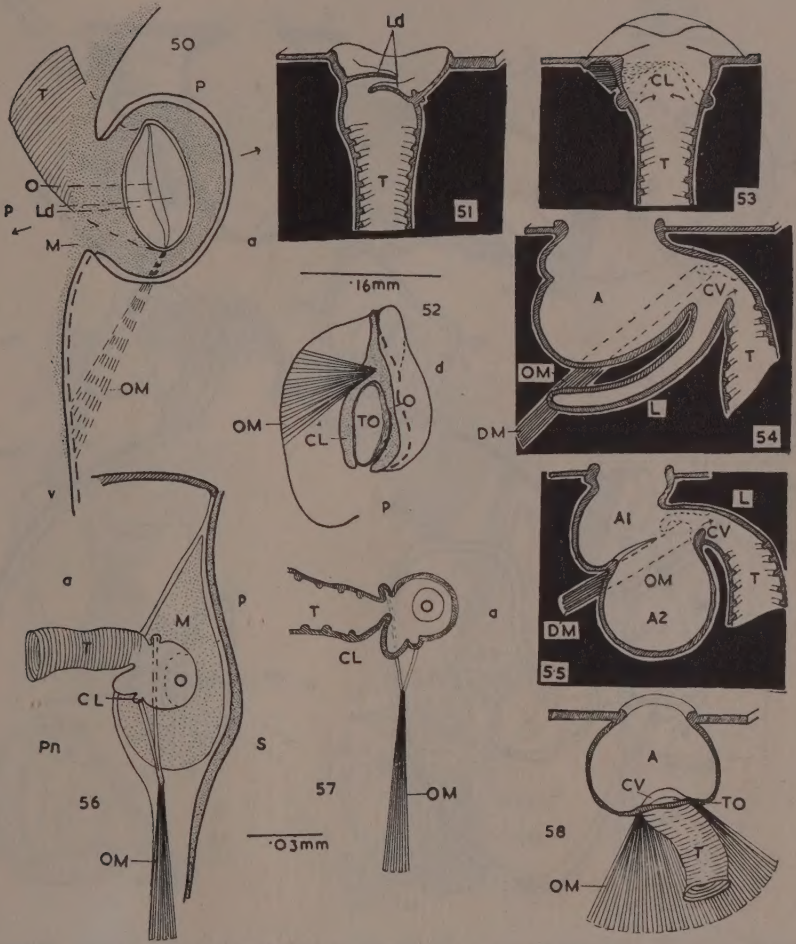
Fig. 41 (*b*).—*Torymus cingulatus* Nees: Gastral spiracle, internal side view.

FIGS. 42–44.—*Exallonyx* sp.: (42) Diagrammatic sectional view of anterior thoracic spiracle; (43) the same of posterior thoracic spiracle; (44) propodeal spiracle, (*a*) external view; (*b*) schematic sectional view in the plane indicated.



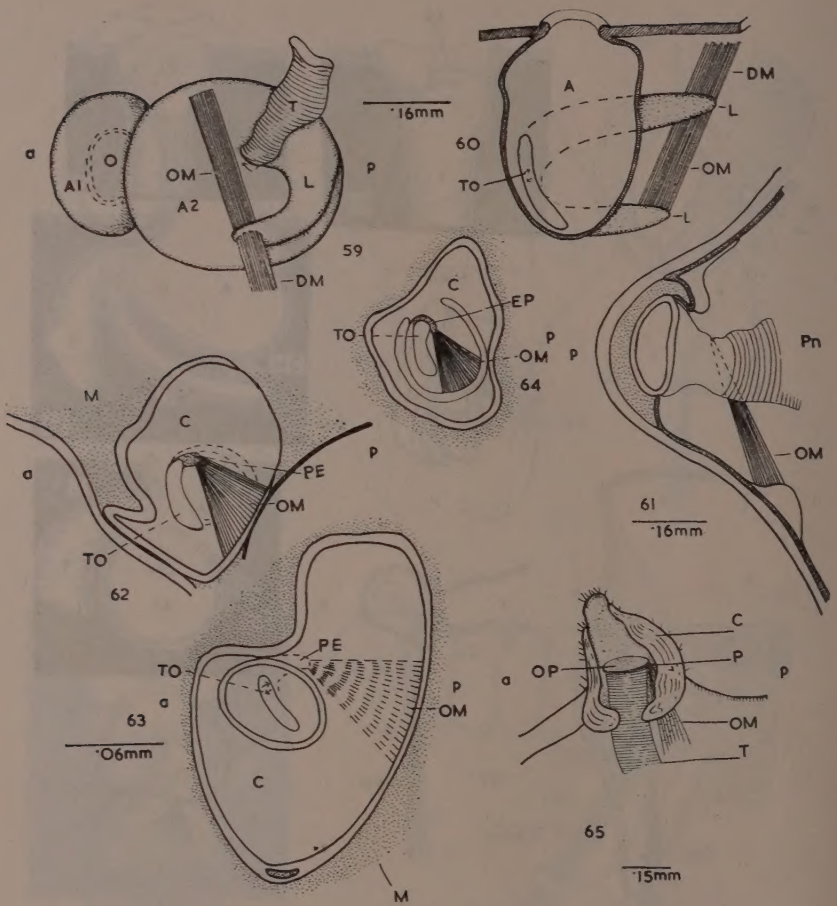
FIGS. 45–47.—*Chrysis ignita* (L.): (45) Anterior thoracic spiracle, internal view; (46) posterior thoracic spiracle, internal view; (47) third gastral spiracle, diagrammatic sectional view.

FIGS. 48–49.—*Myrmica sabuleti* Meinert: (48) Anterior thoracic spiracle, (*a*) external view: (*b*) internal view; (49) third gastral spiracle, internal view.



FIGS. 50–55.—*Lasius fuliginosus* (Latreille): (50) Anterior thoracic spiracle, external view; (51) the same, schematic sectional view; (52) posterior thoracic spiracle, internal view; (53) the same, diagrammatic sectional view; (54) propodeal spiracle, schematic sectional view; (55) third gastral spiracle, diagrammatic sectional view.

FIGS. 56–58.—*Formica fusca* L.: (56) Anterior thoracic spiracle, internal view; (57) the same, schematic sectional view; (58) posterior thoracic spiracle, diagrammatic sectional view.



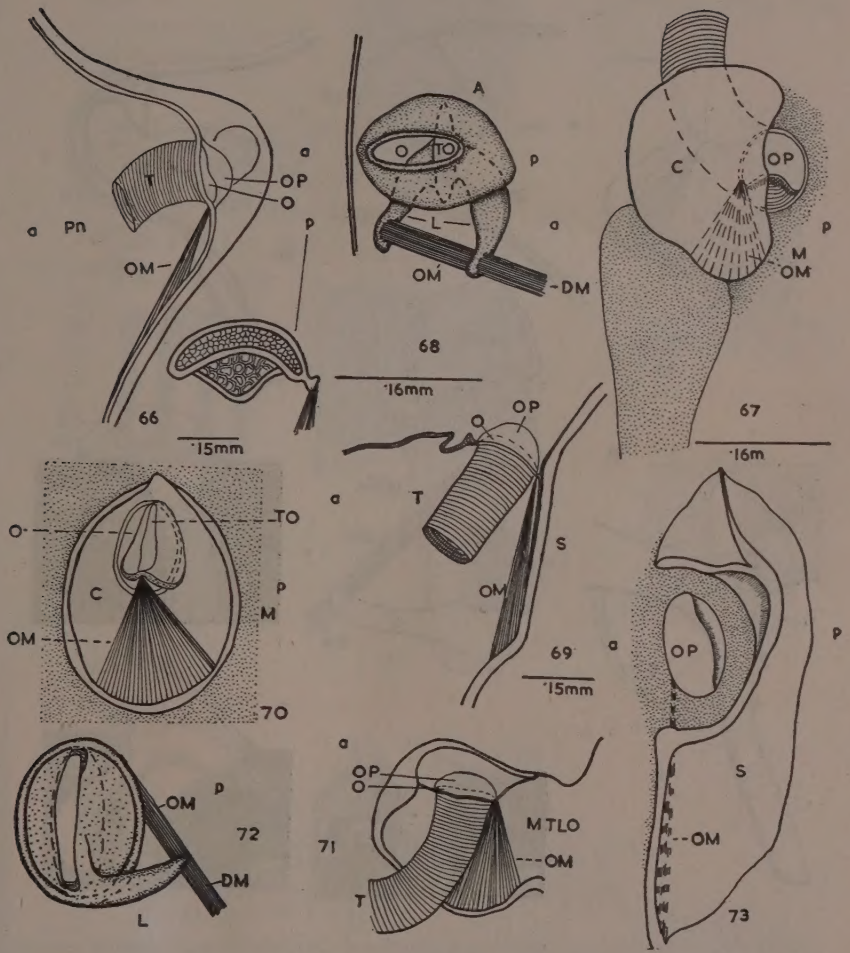
FIGS. 59–60.—*Formica fusca* L.: (59) Fourth gastral spiracle, internal view; (60) propodeal spiracle, diagrammatic sectional view.

FIGS. 61–62.—*Priocnemis exaltatus* (Fabricius): (61) Anterior thoracic spiracle viewed from inner side of pronotum; (62) posterior thoracic spiracle, internal view.

FIG. 63.—*Pompilus plumbeus* (Fabricius): Posterior thoracic spiracle, external view.

FIG. 64.—*Ceropales maculata* (Fabricius): Posterior thoracic spiracle, internal view.

FIG. 65.—*Vespula germanica* (Fabricius): Posterior thoracic spiracle, internal view with membrane around the collar removed.



Figs. 66–68.—*Ancistrocerus trimarginatus* (Zetterstedt): (66) Anterior thoracic spiracle viewed from inner side of right pronotal lobe; (67) posterior thoracic spiracle, external view; (68) third gastral spiracle, outer view.

Figs. 69–70.—*Astata boops* (Schrank): (69) Anterior thoracic spiracle, internal view; (70) posterior thoracic spiracle, internal view.

Fig. 71.—*Podalonia viatica* (L.): Posterior thoracic spiracle viewed from inner side.

Fig. 72.—*Crabro cribrarius* (L.): Second gastral spiracle, inner view, open.

Fig. 73.—*Hoplocrabro quadrimaculatus* (Fabricius): Anterior thoracic spiracle, external view.

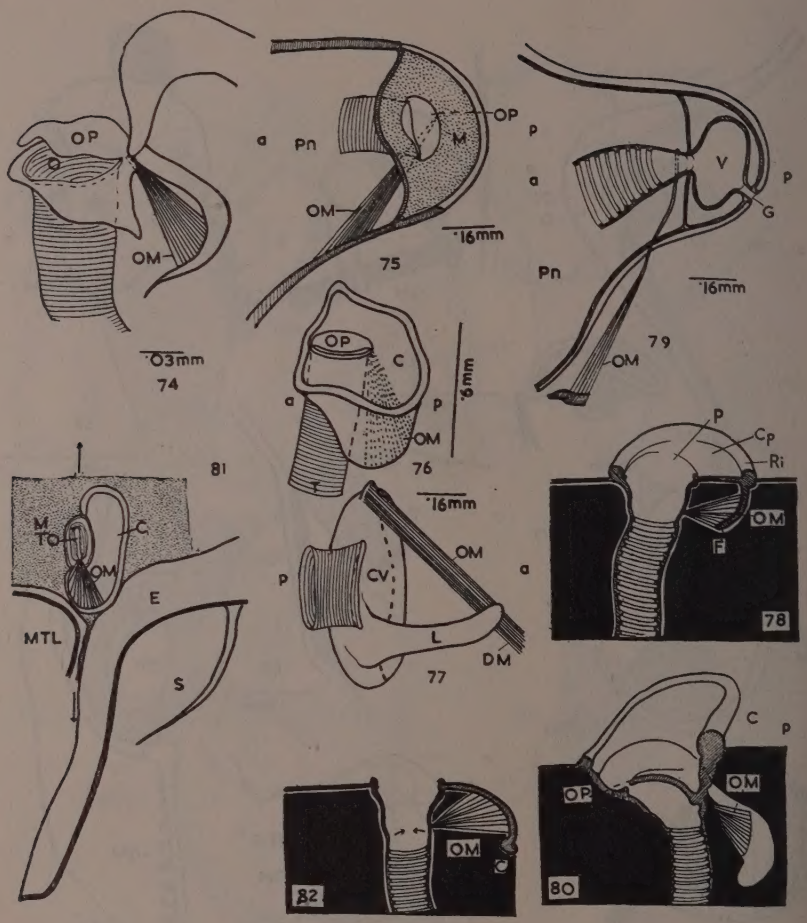


Fig. 74.—*Hoplocrabro quadrimaculatus* (Fabricius): Posterior thoracic spiracle, internal side view, membrane around the spiracle removed.

Figs. 75–77.—*Colletes similis* Schenck: (75) Anterior thoracic spiracle viewed from inner side of right pronotal lobe; (76) posterior thoracic spiracle, external view with membrane around collar removed; (77) propodeal spiracle, internal view.

Fig. 78.—*Sphecodes* sp.: Second thoracic spiracle, schematic sectional view.

Fig. 79.—*Panurgus banksianus* (Kirby): Anterior thoracic spiracle, diagrammatic sectional view.

Fig. 80.—*Megachile argentata* (Fabricius): Posterior thoracic spiracle, diagrammatic sectional view.

Figs. 81–82.—*Stelis aterrima* (Panzer): (81) Posterior thoracic spiracle, internal view; (82) the same, schematic sectional view in the plane of the arrow.